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BLISTER CANKER OF APPLE AND ITS CONTROL

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EXCELSIOR

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SUMMARY

Data are presented which establish the pathogenicity of ***Nummularia discreta*** (Schw.) Tul., as the causal agent of lesions occurring on the apple and commonly known as the blister canker.

At present the disease is not so important economically in New York as in the middle west, but under certain climatic conditions it may become quite destructive.

The disease may manifest itself in several types of cankers designated as staghead, yellow streak, sunscald, and the enclosed and common forms.

The development of natural and artificially induced cankers has been studied both in the greenhouse and in the field, and the fact established that the apple is most susceptible to infection at the time of new growth in the spring.

The fungus may also infect the wood parasitically, yet show no canker formation. Here the presence of the fungus can be detected by the formation of dark brown streaks in the wood which are surcharged with sap having an odor similar to that accompanying fermentation. The discoloration of the duramen or natural heart wood is not due to the invasion of the fungus altho associated with it.

The disease is disseminated chiefly by means of ascopores normally discharged the latter part of August, but which may be expelled until the following summer. Generally two years are required for the ascopores to reach maturity.

The control of the blister canker is dependent upon certain environmental factors, ***viz.,*** location of the orchard, soil conditions, rainfall, orchard sanitation, pruning, spraying, variety, overbearing, and age of host. Shellac followed by coal tar was found to be the most satisfactory dressing for pruning wounds altho no covering will

adhere to duramen that exudes sap and it was found impossible to keep wounds absolutely free from fungi with any method of treatment.

The mountain ash and other hosts must be considered as possible natural sources of infestation and centers of dissemination of the spores. Proximity to the bark of the discolored streaks in the wood and the rapidity of callus formation determined the success of canker treatment more than did any surgery or the application of any covering or spray material to the wound.

INTRODUCTION

Staghead or the dying of apple branches has been of such economic importance in New York that many investigators have sought the exact cause of the injury. The causal agents of winter injury, blight, root rot, and European and black rot canker have been studied at periods when, singly or combined, they appeared to predominate. Some of these have subsided, while seemingly others have been eliminated only to reappear suddenly with increased vigor. Every orchardist can recall past epiphytotics that have appeared, sojourned, and then vanished as rapidly as they appeared. Such cyclic periods, if the causal agent is always present, are dependent upon the physiological changes of the host and its environment.

The work reported in this bulletin shows that the fungus *Nummularia discreta* (Schw.) Tul. is one more agent causing the dying of apple branches. This organism, which produces lesions on the apple branches, aptly known as blister canker, has been under observation by the writer in New York since 1912. The study was prolonged in the hope that each successive year might be more favorable for canker development than its predecessor, but the writer was largely rewarded with disappointment, altho the year 1915 was the most favorable for the study of the fundamental factors involved. Nevertheless, valuable facts were recorded which would have been overlooked had this study been undertaken in an epiphytotical season. At no time during this study was the fungus considered as destructive as it had been previously, or as prevalent as it was reported to be from other fruit growing districts. With the exception of the year 1915, when the fungus threatened to become a serious consideration, the parasite could be considered as existing in a state of comparative

dormancy. It is evident that, under different environment, it would suddenly have left that state and entered a period of maximum destruction. The evidence shows that in the last 30 years there have been at least two such periods when the blister canker was a grave problem to the orchardists of New York. It is to be expected that such environmental conditions may again prevail in this State. However, enough information is at hand to enable us to predict when the blister canker may again become serious, and to know what precautionary measures may be taken to reduce the injury to a minimum.

LITERATURE

The early literature pertaining to *N. discreta* (Schw.) Tul. consists of mycological descriptions that have only an historical interest, altho they incidently show its wide distribution and cosmopolitan nature. In 1831 Schweinitz (32),[1] calling the fungus *Sphaeria discreta* Schw., described it as occurring on the trunks and branches of the apple. He states that he once mistakenly distributed to friends the rare Carolinian Sphaeria as *discincola,* which he described in 1822 (31). The only available description of this species by Fries (9) in the same year is too meager to be satisfactory. The Tulasne brothers (34) carefully figured, described, and gave the name *Nummularia discreta* to a fungus which they found on *Sorbus hybrida* in the suburbs of Paris. They also state that the description of *Sphaeria discincola* Schw. by Fries does not agree with their material, but that the American specimens received from Schweinitz under that name fit the description. They examined Ravenel's (28) specimen of *Sphaeria* (*Diatrype*) *discreta* Schw. on *Magnolia glauca* from South Carolina, and also mention Montagne (21) as describing it from French Guiana. In Germany, it was reported by Nitschke (23) on apple and by Fuckel (10) on *Betula alba.* Jaczewski (18) found it on *Pyrus malus,* Sorbus, Ulmus, and Betula in the neighborhood of Berne, Switzerland. In 1873 Peck (27) reported this fungus on apple under the name of *Diatrype discreta* Schw. from Poughkeepsie, Bethlehem, and Guilderland in New York. Ellis and Everhart (8), in 1892, record *N. discreta* on apple and service berry (*Amelanchier canadensis*) from Newfield, N. J. They also report it as found on apple by Farlow in New England, and on honey locust (*Gleditsia*

[1] Reference to Literature Cited, p. 68.

triacanthos) by Morgan from Ohio. They refer to Cooke (4) who throws further light on the earlier specimens of *N. discreta* by saying that the specimens of *Sphaeria discincola* Schw. in the Kew Herbarium, figured by Currey (7) do not differ from *S. discreta*. Saccardo (30) mentions *N. discreta* as occurring on Malus, Sorbus, Cercis, Magnolia, and Ulmus in Germany, Italy, North Carolina, Alabama, New York, and Cuba.

Hasselbring (14) in 1902 called attention to the seriousness of *N. discrēta* as a parasite on apple trees in the state of Illinois. Selby (33) and the writer (11) have noted this disease in Ohio, and the former reported a survey of 500 acres of orchard in southeastern Ohio wherein 18 per cent of the trees showed the fungus present as a canker. Cowart (6) investigated the parasitism of the fungus by successful inoculation on apple trees. Recently Cooper (5) studied the fungus and the canker it produces in Nebraska. Others have reported the fungus from Iowa (26, 13), Indiana (24), New Hampshire (2), New Jersey (3), and New Mexico.[2]

DESCRIPTION OF CANKERS

N. discreta has never been observed to cause a leaf spot or the decay of the fruit of the apple. Attempts to induce leaf spot formation have given negative results, and the inoculation of growing and mature fruit did not produce decay. It is believed, therefore, that the fungus acts only as a wound parasite and that its economic importance lies in the formation of cankers.

The term canker is applied to any abnormal or diseased condition of the bark that involves more or less of the surrounding wood, and the blister canker is but one of several cankers occurring on apple trees. A blister canker may be quiescent at one period and suddenly enlarge, while a similar canker on another tree or even on the same tree may behave differently. It may thus assume various forms depending somewhat upon its position on the tree, its age, and its environment.

It is impossible to predict how the host and the parasite will react upon each other and hence a description involves conditional statements to a large degree. Some of these forms are here described,

[2] From U. S. Plant Disease Survey.

but as the fungus is progressive it is natural that it may assume several forms in its history.

STAGHEAD

The first intimation the orchardist may have that his trees are abnormal is the discovery that some branch is devoid of its foliage. Such a condition is known as staghead and *N. discreta* is but one of the causal agents. A staghead may occur anywhere on the tree, but it often begins on a secondary branch which is shaded by a larger lateral branch. It may comprise a branch less than an inch in diameter projecting prominently from a mass of green foliage, or it may involve one or more of the scaffold branches that have been killed. This stage is clearly shown in Plates I and II.

An examination of the staghead may reveal the presence of a well developed canker, but more often there is to be observed only the pruning wound thru which the fungus entered. It may show withered bark varying in color from a chestnut to a dirty brown with more or less loose periderm hanging in shreds. In the latter case the bark soon weathers away exposing the bare wood. After a rain the newly killed bark at the proximal end retains a great deal of moisture thus making it mushy and readily separated from the wood. Stromata may be lacking and only secondary fungi may be identified. Sometimes the cream-colored mottled interior bark can be observed, but more often it is necessary to culture the diseased wood in order to diagnose the disease correctly.

YELLOW STREAK

The term yellow streak is applied to the edematous, yellowish areas or streaks that are formed in the bark as a continuation of a staghead or canker. There are actually two forms of yellow streak, the one producing a thick edematous small area usually near the apex of a canker and the other forming a long, narrow, yellowish streak of diseased bark. Other agents besides *N. discreta* produce a similar reaction. The condition is manifested by the papery periderm becoming loosened from the bark, the presence of air beneath imparting a yellowish tinge to the lesions. The streaks may extend for long distances as shown in Plates II and V. The periderm is easily torn into shreds thus exposing the edematous tissue which readily cracks on desiccation. The bark separates from the

wood and may be removed in long strips. The following spring a callus forms along the parallel borders of green bark and this, in turn, may be killed by the further advance of the margin of the canker. When such lesions extend to the trunk of the tree they may be incorrectly diagnosed as the result of bacterial blight or winter injury, but the presence of the canker about the pruning wound soon dispels such an idea. The formation of the yellow streak is so rapid and occurs so late in the season that stromata do not usually form therein. Yellow streak was most abundantly observed on Grimes Golden altho it was found on other varieties as well.

SUNSCALD

The writer has repeatedly observed that the dead bark at the center of a lesion on the trunk of a tree may be rough and brittle. The gray to black center has a margin of bright red which is bordered by the healthy green bark. These areas increase from time to time with little indication of callus formation. It is clear that perennial enlargements such as these are not due to winter killing and, sooner or later, they develop into the yellow streak or common form of canker. This condition may be considered as a secondary infection following winter injury or a wound. Plate VIII shows a Ben Davis tree, inoculated April 28, 1917, which has formed a canker of this type. The tissue above the canker may be depressed because of the inhibitory effect produced by the presence of the fungus upon the cambium activity. This is clearly shown in Plate IX, *C*.

ENCLOSED FORM

The rare enclosed blister canker is a form similar to that found in sunscald altho it resembles the European canker in that successive calluses may be killed. The center of the canker is depressed, due to the more or less concentric, irregular, terraced calluses which have been killed in the progress of the disease. The calluses may not be continuous, and are not stimulated to grow outward as in the case of the European canker. The irregularity may be accounted for by the fact that, in some seasons, the callus is not uniformly killed on all sides of the lesion. Healthy callus may continue to form for from two to six years tho ultimately it may be killed by unfavorable conditions. These cankers are formed about wounds made on the

lower branches during cultivation or center about small pruning wounds situated on very large branches. Stromata are seldom found in this form altho occasionally a few are present in the lesions.

COMMON FORM

The common form of the blister canker is found centered about a pruning wound and is readily recognized if the stromata are present. The newly formed cankers are semicircular (Plate VII, *A*) to V-shaped and of a dark green color which changes to chestnut. Concentric darker lines resembling those made by a pencil (Plate XII, *B*) indicate the progress of the disease in the alternating cool and warm days of spring. These lines disappear or may be entirely lacking if the advance of the fungus in the bark is uninterrupted. The desiccation of the diseased bark and the formation of the callus at the margin of the canker produce a bark tension which results in a rupture at the callus border. This crack or line of demarcation first begins at the sides and later forms at the apices of the cankers. In some cankers this line is complete, while in others it is broken at the ends where there may be a slight depression of the healthy bark as illustrated in Plate IX, *C*. The older cankers take on various shapes and the sizes range from a few centimeters to several meters in length. The diseased bark may be more or less cracked and loosened from the wood (Plate VI, *A*), and the yearly increases of the canker can be followed. In a slow-growing natural canker the wood beneath the dead bark is more or less desiccated, but as the region of the healthy bark is approached the wood beneath contains a greater amount of water and is of a darker brown color. A secondary canker may sometimes form at a distance of a meter or so beyond the primary canker and grow independently for several years finally uniting with the primary lesion. Such cankers need not necessarily have their origin at a pruning wound, but may form in the healthy bark. To this type the term island canker is applied.

Intermittently distributed circular or oval areas of discolored bark surrounded by healthy green bark (Plate VI, *B* and Plate XI, *B*) may also be observed as an extension of a canker. The stromata are readily produced in this type of canker, especially on that portion of the lesion killed early in the growing season.

DISTINCTIVE CHARACTERS

When the stromata are present, no difficulty exists in recognizing the disease. The circular to orbicular discs, closely resembling thick nail heads and which protrude from the wood, can be recognized readily. The bark shows areas of cream-colored mottled tissue which may form in more or less parallel arrangement. The dark brown discoloration of the wood in the form of streaks, which may extend for long distances, is another feature. However, when stromata are lacking, the only positive means of identifying newly formed cankers is to culture the wood about the discolored streaks.

NAME

To distinguish this canker from the black rot, Hasselbring (14) in 1902 applied the name Illinois apple tree canker. However, this name does not convey any descriptive features, nor has the canker been limited to Illinois so that the more descriptive name, blister canker, has gradually superseded it. Not only do the stellar openings exposing the stromata produce a blistered effect, but edematous vesicles and an edematous condition of the bark are frequently observed as follows: (1) Enlarged lenticels and edematous pustules ranging from 3 to 10 mm. in diameter may form about inoculations or cankers. (2) After a period of drought large areas of edematous tissue may develop about the diseased bark. (3) The edematous nature of the tissue and the tearing of the loose papery periderm presents a blistered appearance, so that the disease is aptly named.

PREVALENCE OF THE DISEASE

GEOGRAPHICAL DISTRIBUTION

Review of the literature shows that *N. discreta* is widely distributed in Europe and America. In the United States it is most abundant in the Mississippi River Valley where extreme continental climatic conditions may prevail. Its range coincides with the region known as the Ben Davis belt which includes the apple growing districts of Arkansas and Oklahoma, northward to the southern part of Nebraska, and then eastward. It is present to a moderate degree in the region known as the Baldwin belt, including New York, the northern portion of the states of Ohio, Indiana, and Illinois, and the territory to the north. In these last named states it is abundant, especially

in the southern section, becoming less so as one goes northward. The writer has found the blister canker in Wisconsin, Illinois, Ohio, and, to a varying degree, in the orchards of western New York and in the Hudson River Valley. It does not appear to be localized about a common center, but is distributed irregularly thruout an infested orchard.

ECONOMIC IMPORTANCE

As the activity of *N. discreta* is dependent upon its environment, it is but natural that our estimation of the importance of the disease varies considerably. In Ohio the writer has observed orchards in which 90 per cent of the trees have perished from blister canker. However, this is exceptional for Selby (33), in a survey of plant diseases in Ohio in 1912, found that only 18 per cent of the apple trees were attacked by the fungus.

Under present conditions the disease is of much less importance in New York, and in no case since 1912 has it been so severe as it is in the Ben Davis fruit belt.

PAST EPIPHYTOTICS

Reference to the literature shows that this perennial disease has been more prevalent at some periods than at others. Schweinitz (32) states that the fungus was found on the apple, altho rare, in North Carolina. Hasselbring (14) first observed that the disease reached epiphytotic proportions on the apple in southern Illinois in 1901, altho at that time cankers of from 5 to 6 years of age were found. In 1911, the writer (11) observed a similar situation in southeastern Ohio. Greene (13) states that the blister canker was found to a limited degree in the summer of 1911, but that in the summer of 1912 " literally thousands of trees as well as a great many entire orchards were practically destroyed by this trouble in many parts of Iowa." In New York, the writer observed evidences of two epiphytotics, one centering about the years 1897 to 1900 and the other from 1907 to 1909. Dying branches from the latter period were common in 1912 (Plates I and IV), while those dating from the earlier period were less abundant (Plate III).

RELATION TO PRECIPITATION

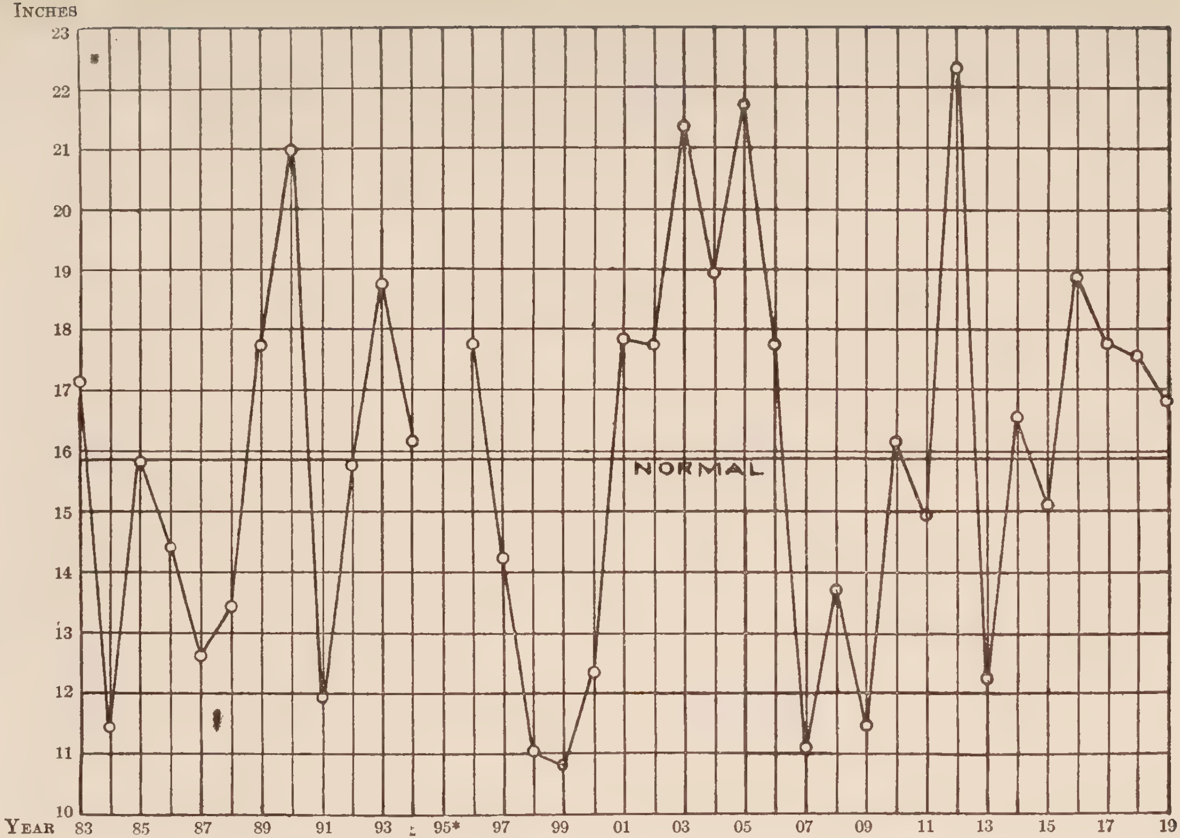
A correlation between the rainfall and the production of canker was observed thruout the study. It was found that a single period

of drought may be influential in causing the spread of the canker, but its destructiveness attained an epiphytotic condition only when the water table was lowered considerably by the cumulative effect of several periods of dry weather. For this reason, the precipitation for a certain month may have little significance in itself, but when considered in relation to that of previous months or seasons it may be all-important in predicting future epiphytotics.

An examination of the meteorological records of the Station[3] furnishes some valuable information on this question, and Fig. 1 shows the yearly variation of the total rainfall from May 1 to October 1, 1883 to 1919, inclusive, based on these records. During the period covered by this investigation the years 1913 and 1915 showed a subnormal precipitation. The rainfall of 1913 was well distributed and did not produce as great an effect as would be expected because the water level of the soil was comparatively high due to the rains of early spring and the previous year, and a drought effect was not observable. In 1915, during the blooming period and the setting of the fruit, a drought occurred which stimulated canker formation. In Ohio, in 1911, a similar period of drought prevailed at the time of blooming with a like production of canker. During those years the cankers continued to enlarge thruout the growing season. Thus a lack of rainfall in April, May, and June may stimulate the activity of the fungus so as to produce epiphytotic conditions.

The graph shows that previous to the time of this study there existed a correlation between the lack of rain and the time at which many of the older cankers apparently were formed. It shows three distinct epiphytotic periods 1884–88, 1897–1900, and 1907–09, the two latter still showing their effect in 1912. That the disease was present in the earlier period is inferred, for Peck (27) reported it present in this State in 1873. It appears that the influence of the drought from 1897–1900 was observed in several parts of the country. Walker (35) attributed the dying of the trees in Arkansas partly to drought, and his photographs show the effects of blister canker. Hasselbring (14) observed the part which the fungus played in the killing of the trees in southern Illinois. Paddock (25) studied the dying of apple branches in New York due to the fungus *Sphaeropsis malorum*. He experienced no difficulty in producing cankers from

[3] See Annual Reports.



*Data for June and July not available.

FIG. 1.—GRAPH SHOWING YEARLY VARIATION OF TOTAL PRECIPITATION FROM MAY 1 TO OCTOBER 1, 1883 TO 1919, INCLUSIVE.

inoculations, whereas later investigators, working under conditions of heavier rainfall, had slight or even negative results. Paddock, no doubt, overlooked the presence of *N. discreta* in the orchards about Geneva, for some of the cankers of today have a history (Plate III) that antedates 1900. The effect of the lowered water level of 1907–1911 was observed in Ohio (11, 33), Iowa (26, 13), and Nebraska (5).

RELATION TO SOIL CONDITIONS

Wilkinson (36) points out the fact that with given temperatures some varieties of apples are more adaptable to certain soils than others. The Northern Spy, for example, thrives best on heavy water-retaining soils, while the Ben Davis prefers a lighter soil. *N. discreta* is more active in orchards growing on poor, shallow soils, on sod, or on uncultivated land and hillsides. The Volusia soils may have a rock or impervious clay (hardpan) subsoil, which, at the first indication of dry weather, puts the trees under drought conditions. In Ohio (1), such trees readily respond to fertilizers, while the New York orchards on richer soil do not respond to such treatment (16). In one of the latter orchards two trees were found to have been attacked by blister canker. On one tree the canker was only 15 cm. long; while the other tree showed cankers on three 8-cm. branches, one of which was girdled in 1918. The old Station orchard, on similar soil, was destroyed in 1917 because it was badly cankered. Out of 123 trees examined, 18 showed blister cankers ranging from several centimeters to 4 meters in length. (See Plate IV.) On these trees stromata were formed, while 22 trees showed blister cankers in which they had not formed. After the trees were dynamited it was found that small cankers near the tops of the trees had been overlooked. In 1912, in a 40-year-old Baldwin orchard, on similar soil, none of the 40 trees examined were free from the blister canker. Some of the trees were dead, others were dying, while still others (Plate III) showed cankers in all stages of development. In these cases, the trees were located on soil rich in the chemical constituents necessary for growth.

The question naturally arises whether sod or cultivated orchards suffer the most from blister canker. No definite data are available on this subject, altho Hedrick (17) noted a greater amount of dead wood on trees grown on sod. In 1917, three years after Hedrick's

experiment was terminated, the writer visited the orchard to diagnose, if possible, the cause of the dying of the branches. Blister cankers were found in about equal numbers on the trees in the various cultural plats and, in some cases, their origin dated back several years. It is assumed that the blister canker was partly to blame for the greater number of dead and dying branches in the sod plats. These observations strengthen the general impression that orchards on sod show more canker. This may be partly due to the fact that the orchardist who practices sod culture is often tempted to neglect the orchard, and to omit pruning and general spraying.

RELATION TO AGE OF TREE

The fungus generally does not attack young trees, but makes its appearance at about the time the tree begins to be profitable. This may be due to the greater ease with which the fungus can invade the host at a time when the fruit is making demands on the water and food supply which normally was stored and produced new woody tissues. From results of inoculations, the writer must conclude that the newly set trees are very susceptible; while those with well established roots are rarely killed outright, but require several years to produce a large canker. (See Plate VIII.) In the case of the Ben Davis, 10- to 20-year-old trees are subject to attack; while in other resistant varieties canker is found on the older trees only, which, because they had passed thru various adverse periods, finally became infected.

It appears that the vigor of the tree in itself is not a safeguard against infection. The writer has repeatedly observed, in fertile pockets along hillsides, Ben Davis trees which were more diseased than those less favorably situated. On the richer soil, the trunks of the trees had a greater diameter, the spread of the branches was wider, and the foliage larger and darker green than that of nearby trees, nevertheless the cankers were more numerous and larger than on poorer, smaller trees of the same age and variety.

OVERBEARING

Trees which have borne to excess appear subject to canker. Such trees may have broken branches thru which the fungus can enter, or the superabundance of fruit may be an indication of some injury to the roots for it is generally known that an injury to the trunk or

the roots of a tree may stimulate the formation of fruit. The excess fruit requires an unusually large amount of the food and water which, under normal conditions, is diverted to the building of woody tissue. The following season, these trees are handicapped and make poor radial growth, and are thus less able to withstand the advance of the fungus in the wood and bark.

VARIETIES ATTACKED

The blister canker has been found on 40 varieties of apples grown in New York and it appears that but few of the standard varieties are free from it. They are not all attacked with equal severity and some of the newer varieties have not reached a sufficient age nor withstood climatic variations long enough to determine their susceptibility. When the Ben Davis and the Baldwin are grown side by side the former shows a preponderance of canker. The Red Astrachan is not only subject to the blister canker but to the European canker as well. In New York, the Northern Spy and Northwestern Greening show a high degree of resistance, altho they are not immune. Old trees of apparently resistant varieties have passed thru epiphytotics uninjured, while nearby Baldwins were killed or suffered greatly. It is difficult to state just what varieties are resistant or immune, for the condition is transitory or temporary, and dependent upon the environment. Western New York, with its well-distributed rains, does not appear to be the most favorable location in which to test varietal susceptibility to blister canker.

RATE OF CANKER ENLARGEMENT

Variations in the behavior of cankers in different years would be expected, but in the same season some cankers are active while others are quiescent. For several years the writer has selected typical cankers and inserted tacks in the margins, which were observed at various dates. On a Collamer apple tree grown on the Station grounds (Plate IV) the boundaries could be traced up to 1909 when a pruning wound 8.5 cm. in diameter was formed by the removal of a dead branch. Beginning at the pruning wound the positions of strings connecting the tacks have been measured, the distal measurements being made on the central branch. The results are given in Table 1.

TABLE 1.— MEASUREMENTS OF CANKER ENLARGEMENT.

String number	Year	Notes	Distance from pruning wound	
			Distal	Proximal
			cm.	*cm.*
1........	1909	Callus killed........................	0.2	0.6
2........	1910	Area arc-shaped......................	1.0	2.5
3........	1911	Area V-shaped........................	2.5	9.0
4........	1912	Stromata formed first time............	5.5	19.0
5........	1913	Stromata abundant....................	19.0	25.0
6........	1914	Outlined April 27....................	25.5	38.0
7........	1916	Outlined August 31...................	65.0	45.0
	1917	Outlined Oct. 21, not photographed......	79.0	49.5
Average growth for 9 years............................			8.7	5.5

On the branch to the left (Plate IV) lines 5, 6, and 7 extended 15, 30, and 52 cm., respectively, from the pruning wound. On August 31, 1916, all but 1.5 cm. of the bark was girdled and in December the girdling was completed. The branch had produced an abundance of fruit which was badly spotted with the physiological fruit pit. After the leaves were shed, yellow streak developed (Plate V), and on May 9, 1917, this streak was 3 meters long. On October 21, 1917, the girdled branch bore foliage and undersized fruit holding tenaciously to the fruit spurs, indicating that the branch was able to supply the leaves and fruit with necessary sap which was transported thru the diseased wood.

Similar observations were made on a Baldwin tree growing on the Station grounds. (See Plate III.) The large pruning wounds were formed May 6, 1914, by the removal of dead blister-cankered branches. The wounds were treated with carbolineum followed by tar. The four outer strings outline the margins of September 1, 1916; June 6, 1916; July 3, 1914; and May 6, 1914, respectively. By following the old calluses, 15 boundaries were traced with the central of the three branches as the source of original infection. On October 31, 1917, a section of the trunk was made 30 cm. above the ground and 17 annual rings were found between the healthy tissue and the primary lesion. This canker, therefore, originated prior to 1900, and during this time one of the margins expanded 26.5 cm. from the center of the lesion, or an average tangential growth of 1.55 cm.

per year. Whether or not the margins ascend or descend more rapidly depends upon the position of the canker on the tree. Around artificial inoculations, the cankers developed at about the same rate in either direction.

TIME OF CANKER ENLARGEMENT

Natural cankers may enlarge their margins at any time during warm weather from March to December. Whether a particular canker enlarges its margin depends upon the proximity of the mycelial strands to the bark and the amount of intervening callus or annual wood. However, there are periods when cankers have a marked tendency to enlarge. Cankers rarely enlarge early in the spring before the buds have begun to swell or before there is any indication of the awakening of the cambium. In a dry spring, as in 1915 and to a lesser degree in 1918, the cankers enlarged while the blossoms were in the closed cluster stage and continued into June until the radial growth was sufficient to occlude the fungus. If there is an abundance of rain, the canker and stag-head formations may be postponed until the first dry days of July. The cankers enlarge slowly during a period of summer drought, and show a considerable increase of the margin in a period of heavy rains following a period of drought, when yellow streak may be evident. During the September rains edematous tissue may form along the margins and, just prior to the falling of the leaves or even after the leaves have shed, yellow streak is commonly formed.

The V-shaped lesions at the proximal and distal ends of a pruning wound are often erroneously attributed to the drying out of the bark. Only in a spring of limited rainfall, as in 1915, were areas formed that could be attributed to drought. At the same time natural cankers were forming similar areas. Some writers, observing these areas, have advised that all wounds should be trimmed to a V at the time of pruning. This, however, is needless and only delays the healing of the wound. In such a year the formation of the stromata or the cream-colored mottled bark clearly demonstrates the presence of *N. discreta*.

Generally, cankers resulting from inoculations formed at the time of the awakening of the cambium, that is, when the flower buds are in the closed cluster stage. (See Plate X, *B*.) A canker may form at the end of the blooming period about an inoculation made on the

upper side of a lateral branch out of the direct sap flow, while other cankers on the same tree may be produced earlier. Some branches inoculated in 1915 produced no external canker, but in the autumn of 1917 they shed their leaves prematurely and the bark lost its normal color. After the severe winter of 1917–18 such branches refused to leaf out and resembled the winter injury observed on trees and branches that showed overbearing of fruit the previous year. In 1919, the inoculated branches showed stromata formed at the proximal end of the dead branches, while none were found on those branches which winter killed.

Generally, a lateral branch may be killed before the margin of the canker reaches the branch. Thus in Plate II the branch to the right shows the lower lateral branches exhibiting staghead while the margin of the canker was still 10 cm. away. The branch to the left in Plates IV and V shows the other extreme, for all but 1.5 cm. of the bark was girdled on August 31, 1916, and completely girdled in December. However, on October 21, 1917, the bark and foliage were still green and the undersized fruit was still clinging to the fruit spurs.

HOSTS

The fungus causing the blister canker has been reported on various hosts. Inoculations have shown that cankers may form on the pear, altho natural cankers are rarely found on this host under normal conditions. The Juneberry (*Amelanchier canadensis*) is commonly attacked and the presence of such trees in the woodlot may explain the larger number of affected apple trees near the woodlot than among those further removed. The fungus is more active parasitically on Sorbus than on apple. It causes the staghead and dying back of the mountain ash (*Pyrus americana*) that is so often observed. This tree is found from Newfoundland to Manitoba, southward to New Mexico, and eastward to North Carolina. This region coincides with the range of the blister canker on the apple: The pinnately leaved Sorbi grow best in a cool moist climate, and when grown in a different environment are sooner or later attacked by *N. discreta*.

The line of demarcation between the healthy and diseased tissue in the European mountain ash (*Pyrus aucuparia*) is less distinct than in the apple, but the general appearance of the disease on the former is similar. On the mountain ash the canker enlarges more rapidly,

and the stromata and ascospores are more readily formed than on the apple. The boundaries of the cankers on the mountain ash may not be conspicuous due to the fact that the bark has less tendency to crack than in the apple, the inner bark drying and shrinking away thus leaving the outer papery periderm intact. In 1915, a lesion which had advanced to a length of 10 cm. by March 25, produced stromata by June 14, sloughed away the conidiophore cushion by August 19 allowing a slight spore discharge, and on September 21 the ascospores were heaped upon the stromata and distributed during the autumn and the following spring. Because the mountain ash sooner or later becomes a center of spore discharge, it should not be planted as an ornamental in the vicinity of apple orchards.

CAUSAL AGENT

The dying of apple branches, which now can be ascribed to *N. discreta*, was formerly attributed to various causes. The orchardist, being unable to distinguish between cause and effect, would observe a secondary factor or a manifestation of the disease and consider it the primary cause. Thus, if upon the removal of a diseased branch the sap was observed to have an odor similar to that encountered in fermentation, the branch was believed to have been killed by sour sap. When noted in the spring, the death of the branch was ascribed to winter injury, in the summer to drought, and in the autumn to overbearing. While a large number of apple branches are killed by low temperature, all branches which die at the time new growth begins are not winter killed as there are other agents which produce similar effects at the same time.

The constant association of the fungus *N. discreta* with the blister canker would suggest it as the causal organism. The writer has been able to produce the disease by artificial inoculation of trees both in the greenhouse and in the field when the factor of low temperature was not involved.

Saprophytes or even some of the fungi which are known to produce other types of canker may be associated with *N. discreta* as secondary organisms. In the Ozarks, Roberts (29) has found the spores of the apple bitter-rot fungus (*Glomerella cingulata* [Stonem.] Sp. & von S.) in the blister cankers. In New York, *Schizophyllum alneum* (L.) Schröt., *Valsa leucostoma* (Pers.) Fr., *Myxosporium corticolum*

Edg., and *Physalospora cydoniae* Arnaud (*Sphaeropsis malorum* Berk.) may be present in the older tissue of the canker but the advancing margin shows only the mycelium of *N. discreta.*

ISOLATION

The mycelium of *N. discreta* may be readily isolated in pure form and the following methods have given the best results. The most active and virulent mycelium is obtained from the ascospores which can be taken directly from the perithecium or from the surface of a stroma. Dilution cultures can be made and a single ascospore isolated under the microscope. It has been found that such spores that fail to produce hyphal threads may be stimulated to germinate by placing them in a drop of water containing a thin section of wood. Isolation of the fungus from the conidia can be accomplished, but their small size and the fact that they become fixed soon after being exposed to the elements renders their use impractical. The bark is often contaminated with other fungi and is less satisfactory for isolating the fungus.

In the absence of a stroma, it was found that the small discolored streaks in the wood contained the mycelium in pure form. Small blocks containing a streak about 1 to 2 mm. in diameter were immersed in hydrogen peroxide for one minute and then washed in sterile water. The mycelium continued its growth from the transverse cut end when placed on acidulated nutrient glucose agar. Longitudinal sections of a streak, made under sterile conditions, can be examined under the microscope and the mycelium definitely seen in the tracheal tubes before culturing. Blocks of discolored wood taken from the older portions, which may be confused with the natural duramen, may remain sterile, altho in such wood the still darker streaks may be found to contain the mycelium.

CULTURAL CHARACTERS

In attempting to describe the cultural characters of *N. discreta,* it is difficult, on account of variations, to give a description which will cover all cases. Forms varying in pathogenicity and cultural characters sufficiently to be called varieties or strains are produced by changes of environment. There is even a seasonal factor, for the mycelium is more active in the spring of the year than at other

times. A brief description of the isolated fungus grown from a single ascospore obtained from an apple canker is given below.

1. *Agar (1.5 per cent).*— Mycelium scant, superficial, gray; with few gray masses of conidia formed.
2. *Precipitated cellulose (19).*— Mycelium scant with no discoloration of medium unless desiccated. Conidia generally scarce, altho sometimes abundant.
3. *Cellulose agar (19).*— Growth similar to 1; conidia abundant.
4. *Synthetic agar (19).*— Growth more rapid, denser, and darker than 1; with masses of conidia in groups, giving a flocculent appearance.
5. *Potato starch (1 per cent) agar.*— Growth slow, penetrating entire medium which is turned blue-green to sepia-brown in color; with prominent strands which become flocculent when in contact with the opposite wall of a test tube. Chlamydospores abundant and conidia few or lacking. Flakes of calcium oxalate may form on the surface of the medium.
6. *Potato starch (1 per cent) agar plus small portion of apple twigs.*— Growth less rapid than in 5; medium not pentrated and lighter tawny color. Conidia formed on fleshy stroma which may be produced on the portion of the twig projecting above the agar.
7. *Cellulose, synthetic, agar.*— Mycelium gray as in 1. Conidia very abundant and masses smaller than in 3.

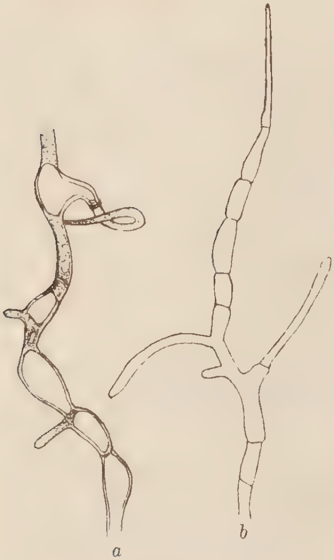


Fig. 2.—Mycelium of *N. discreta*: *a*, on Potato Agar; *b*, on Nutrient Glucose Agar.

Fig. 3.—Conidiophore of *N. discreta* on Nutrient Glucose Agar.

8. *Cellulose, synthetic, potato starch (1 per cent) agar.*— Mycelium more abundant than in 7 with dark sclerotial bodies 3 to 8 by 2 to 5 mm. in size formed at the edges of the medium; medium tawny and conidia absent except on the stroma.
9. *Cellulose, synthetic, glucose (1 per cent) agar.*— Mycelium dense with dark sclerotial bodies formed as in 8 with exudation of liquid from such bodies commonly observed. Medium less discolored than in 8 with conidia present, altho scarce.
10. *Potato starch (1 per cent) glycerin (1 per cent) agar.*— Growth similar to 5; medium a light sepia-brown with an abundance of tan to brown masses of conidia.
11. *Potato agar.*— Growth slow, mycelium thick celled, distorted, enlarged, much branched, matted with cream-colored aerial mycelium; medium dark brown and conidia lacking. (See Fig. 2, *a*.) Length of mycelium 99 microns.
12. *Nutrient glucose agar.*— Growth rapid, strands prominent, gray to ocher and superficial. Aerial mycelium first gray, then white, pink or yellow tinged, changing to olive and then tawny; in old cultures finally gray to brown in color; cottony to flocculent and, when zonate, the concentric rings are a darker brown. Tawny- to cream-colored conidia-bearing stroma 3 to 8 mm. in diameter are rarely formed, later sometimes hollow but without perithecia. Medium discolored, a dark sepia-brown, and conidia formed in 6 to 12 days, measuring 6.2 to 8.8 by 3.2 to 4 microns averaging 6.8 by 3.5 microns, which is slightly larger than normal. Fig. 3 is a camera lucida drawing of the conidiophores and mycelium while growing on nutrient glucose agar. The entire length is 225 microns, and shows more uniform branching than found on the stromata.

The fungus grows well on most of the ordinary media used in the laboratory. On moist corn-meal, oat-meal, and bread, and when combined with agar, the growth of the mycelium is slow, discoloring the medium a blue-green. On autoclaved apple twigs the mycelium grew superficially with occasional surface sclerotia formed as described in 8. On autoclaved bean stems, potato plugs, and beet plugs the growth is slow and on raw potato, carrot, bean pods, apple, and pear the growth was very poor or entirely inhibited. When portions of unautoclaved apple branches (with bark present) were used as a substratum all stages of the fungus observed in the field may be duplicated. By preventing evaporation or by covering the sterilized branch with paraffin, the stromata, conidia, perithecia, and ascopores may be caused to form.

Temperature.— The above descriptions of the cultures were those observed at ordinary room temperatures. In order to determine the thermal range of *N. discreta*, groups of five plates each were incubated at various temperatures and the daily increase in diameter used to measure the rapidity of growth. The averages of each group were plotted to form a curve as given in Fig. 4.

The minimum, optimum, and maximum range of temperature is in the neighborhood of 5°, 25°, and 35° C., respectively. In duplicating such tests, it was found that the more vigorous cultures have a slightly higher maximum than less virulent cultures. That the

fungus may be active in the warm days of winter has been observed in the field and in cultures that had been kept in the open air.

The mycelium in the cultures showed changes in its characteristics at the different temperatures. At the temperature of minimum growth the thin non-strand-like surface mycelium is of a gray color. As the temperature is increased the formation of aerial

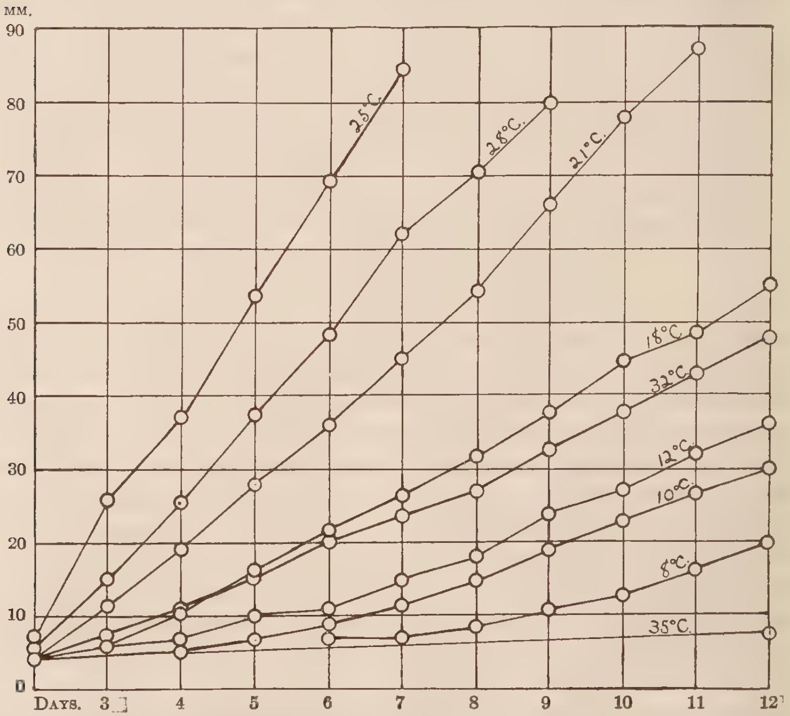


FIG. 4.—GRAPH SHOWING THE RELATIVE GROWTH OF *N. discreta* ON NUTRIENT GLUCOSE AGAR AT VARIOUS TEMPERATURES.

mycelium is stimulated and denser, whiter mycelium is formed with gray mycelium at the border. As the temperature reaches 18° C. the mycelium becomes cottony and may show a pink, olive, or tawny tinge. In the cultures that are zonate, the aerial mycelium may show concentric rings of pink tinge which later turn to brown. Near 25° the aerial mycelium becomes flocculent and may extend 5 mm. above the medium with a loss of the pink color, while at 28°

this color reappears and increases up to 31° when it again disappears. Also at 28° the cottony mycelium is again observed gradually decreasing until, at 32–34° it gives way to the formation of gray surface mycelium similar to that observed at the minimum temperature of growth.

Variations of different strains.— All strains of *N. discreta* do not react alike, nor do they show the same characters at similar temperatures and with the same environment. Newly isolated strains from ascospores or from active tissue show great vigor, producing prominent, radiating strands with an abundance of conidiophores. Strains from an old portion of a canker may show cultures devoid of these strands, but instead, the mycelium is of finer texture and devoid of conidiophores with a tendency to produce a tough membranous layer of surface mycelium. Differences in the cultural characters of the strain isolated from the mountain ash were considered at first as those of a different variety, but inoculation of the apple and mountain ash proved it to be the same as that on apple.

Deterioration of cultures.— From the foregoing it appears that the attenuation of *N. discreta* in cultures was due to age or uncongenial substratum. Fortunately, suitable cultures of various ages were retained which made possible a test of these factors. The history of three of the cultures is given below.

Culture 1.— The mycelium was isolated January 28, 1911, from a canker received from D. F. Jones, Jackson, Ohio. When first isolated the fungus displayed a vigorous growth with the formation of heavy mycelial strands and the production of conidia. In 1912, when inoculated on apple trees at this Station, it produced small cankers. In 1915, when it was again used for inoculation, no cankers formed, altho streaks in the wood were produced. The earlier transfers were made to nutrient glucose agar, and after 1915 the fungus was kept as a stock culture and grown mostly on 1 per cent potato starch agar.

Culture 2.— The mycelium was obtained from a single ascospore isolated August 12, 1915. On October 4, 1915, transfers (third) were made to 1 per cent potato starch agar and the tubes sealed by dipping the cotton plugs in paraffin. One of these cultures, which may be designated as No. 2, remained in excellent condition 3½ years; that is, until March 17, 1919, when subcultures were made for use in this test.

Culture 3.— In 1917, it was observed that a culture originating from the same ascospore as Culture 2, but which had been transferred on nutrient glucose agar several times in the interval of two years, had lost some of its vigor and hence was discarded. Thereupon, a subculture was made on October 30, 1917, from the same Culture 2. The growth obtained showed that the fungus had lost none of its original vigor. During the ensuing 17 months the subculture was transferred many times on nutrient glucose agar. The last transfer of this series is designated as Culture 3. Hence, Cultures 2 and 3 had the same origin and were of the same age, but differed in that the former was grown on potato starch agar without transfer, while the latter was grown on nutrient glucose agar and transferred many times.

On March 17, 1919, actively growing mycelium from each of the above three cultures was transferred to plates containing nutrient glucose agar. The plates were incubated at 25° C. under parallel conditions. The rapidity of growth was considered as an indication of the vigor of the culture and the average of five cultures was used in plotting each curve given in Fig. 5.

The curves show that age in itself was not a factor, but that the substratum appeared to be the determining agent. Culture 2, grown on potato starch agar, showed coarse mycelial strands and an abundance of conidia; while Culture 3, grown on nutrient glucose agar, showed finer strands of mycelium, and was devoid of conidia. The variations observed in different strains isolated from different hosts and from the same host are all within the limits demonstrated in this experiment. The strains isolated from the mountain ash exhibit and maintain a greater degree of vigor in culture than do those isolated from apple. Growing on a less susceptible host (the apple), the mycelium appears to be more readily attenuated. Hence, physiological and morphological characters observed in cultures of *N. discreta*, which by some would be considered sufficient to place them in different varieties or perhaps even different species, are merely the result of the influence of a more or less congenial substratum.

Use of starch agar for stock cultures.— Nutrient glucose agar was long suspected of having a deleterious effect on stock cultures. When grown on such medium, the fungus has been found dead in from 5 to 6 weeks if kept at the temperature of the laboratory during the summer.

In the manufacture of potato starch a sufficient quantity of the chemical constituents are retained to supply the demands of the fungus. This was demonstrated when six successive transfers, covering a long period of time, showed no loss in the vigor of the fungus. Sealing the test tubes with paraffin prevents evaporation,

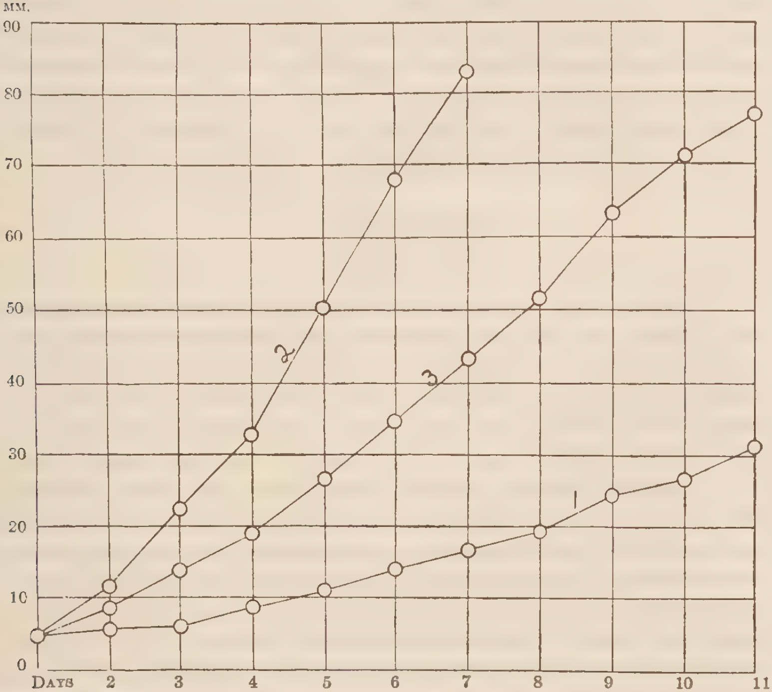


FIG. 5.—CURVES SHOWING RATE OF GROWTH OF THE MYCELIUM OF *N. discreta:* 1. CULTIVATED ARTIFICIALLY FOR 8 YEARS (4 YEARS ON NUTRIENT GLUCOSE AGAR AND 4 YEARS ON POTATO STARCH AGAR). 2. CULTIVATED 3½ YEARS ON POTATO STARCH AGAR. 3. OF THE SAME AGE AND ORIGIN AS 2 BUT CULTIVATED FOR 17 MONTHS ON NUTRIENT GLUCOSE AGAR.

and the formation of chlamydospores or resting mycelium enables the fungus to live passively for long periods. The ease with which this medium is made and the fact that an ice box does not appear necessary in hot weather makes the starch medium especially favorable for the growth of many fungi that are kept as stock cultures.

Digestion of starch.— Starch cultures upon which the fungus is growing, when tested with iodine, show a colorless area beneath the mycelium and for a distance of from 3 to 10 mm. beyond the ends of the hyphal threads. When tested with Fehling's solution, a precipitate of cuprous oxide indicates the presence of sugar. Using brom-cresol purple as an indicator, an acid reaction is observed beyond the boundary of the mycelium. Later the discolored medium loses part of its acidity as the mycelium grows over it. The deep penetration of the mycelium beneath the surface indicates that the fungus utilizes oxygen derived from the sugars formed, and that in certain media only a limited amount of oxygen is necessary.

MORPHOLOGY

STROMATA

The term stroma is loosely applied to the circular or orbicular fruiting mass of bark and mycelium in which the perithecia are enclosed, and which also has on its outer surface a separate fleshy conidiophore layer. The first indication of the formation of a fruiting body may be the enlargement of the lenticels which appear as if they had been induced to increase their size by being placed in a damp atmosphere. In other cases, where the infected bark is still green, the first indication of the stroma may be the formation at a lenticel of a small watery vesicle beneath the periderm. Such areas measure from 3 to 4 mm. in diameter and may be bordered by a band of red pigmented bark. These blisters readily become desiccated and in time the bark loses its green color and dies. Directly beneath the periderm a delicate tawny weft of mycelium is formed which at first is but 1 mm. in diameter, but gradually increases in diameter and in thickness. When about 4 mm. wide, the base and center become sclerotic and may assume a dark blue-green color that later may turn brown but oftener becomes black. A fleshy, succulent, mycelial cushion is formed above this sclerotic tissue, and soon is divided horizontally, forming two layers from which the conidiophores arise on the newly formed opposite surfaces. The outer layer also forms the mechanism for exposing the conidiophore layers to the air. The periderm cracks at a lenticel, due to the pressure exerted by the hygroscopic mycelial cushion, and the periderm is curled outward and finally backward so that thru the

stellar opening which is formed the two layers of tan-colored conidiophores may be observed. Thus two conidiophore layers that were formerly opposite sides of a separation layer now become the outer exposed surfaces. The curled-back periderm (Plate XIII, *B*) is frail and is readily broken or weathered away. On the mountain ash (Plate XII, *A*), the periderm is tougher and remains for a longer period. Any portion of the fleshy mycelium may function in producing conidiophores, which may sometimes be formed in the unexposed ruptures. The conidiophores do not show any uniform system of branching as observed (Fig. 3) when grown on artificial media; but instead, are very irregular, stunted, and more or less branched. They are variable in size and in Fig. 6 the tallest is but 42 microns.

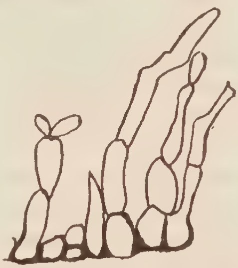


Fig. 6.—Group of Conidiophores of *N. discreta*.

The one-celled hyalin- to honey-colored conidia are abundantly formed, and average 3 by 6 microns, varying from 2 to 4 by 4.5 to 8 microns. In some cases there may be a profuse formation of the fleshy mycelium and upon the irregular surface conidia are produced in abundance.

Many of the stromata never mature, for their development is dependent upon the moisture available in the form of sap or rains which may be absorbed and retained by the stromata. Usually the fleshy conidiophore cushion on the surface of the stroma increases in thickness; while the dark sclerotic tissue beneath also increases in size, leaves its horizontal position, grows vertically to form the boundary of the stroma, and then resumes its former direction of growth and continues as a sclerotic covering to the woody tissue. Generally, this sclerotic tissue penetrates into the wood to the depth of several layers of cells, producing a sclerotic band in the summer wood of the previous year instead of this being formed in the surface layers. The current season's wood, being unaffected, ultimately weathers away. In some cases the sclerotic layer does not penetrate to the wood, but appears to penetrate only to the cambium tissue, and such stromata are readily removed with the bark when it sloughs away. Due to the greater resistance of the sclerotic tissue to the elements, the stromata may remain attached to the wood for from 7 to 14 years. At first they resemble protruding nail heads, and

later a concave stroma, devoid of all bark, resembles the head of a molar tooth. (See Plate XII, *C*.) When the stroma is removed from the wood, the outline of the darker sclerotic tissue is readily observed (Plate XIII, *A*).

The size of the stromata is dependent upon the extent of the sclerotic boundary which, in turn, is influenced by the host, the age and thickness of the bark, and upon the amount of moisture present. They appear to attain their greatest size when grown on the older branches of the mountain ash where they average 9 by 5 mm. in area and $3\frac{1}{2}$ mm. high. When circular, they vary from 3 to 9 mm. and, when orbicular from 3 to 12 mm. with the longest diameter generally parallel with the axis of the branch, altho there are exceptions. (See Plate XII, *C*.) On the apple, the stromata are generally smaller, tho some may be found as large as the largest on the mountain ash. They are more often circular and about 5 mm. in diameter. On the Juneberry they are much smaller, being 3 to 5 mm. in area and $1\frac{1}{2}$ mm. thick. When two or more stromata fuse the size naturally is proportionally increased. The thickness of the stroma shows the greatest degree of variation, being but $1\frac{1}{2}$ mm. thick when formed on the younger branches. With an abundance of moisture the sclerotic tissue is increased by the formation of new tissue which, in turn, increases the height of the structure.

PERITHECIA

The perithecia, or the bodies that enclose the asci and ascospores, have their origin in a group of sclerotic cells that may form just beneath the old sclerotic layer which underlies the conidiophore cushion. Thru the multiplication of these cells the perithecium and its neck are formed. These cells may be hyalin or, if their development has been arrested for a short time, they may become the blue-green color characteristic of the sclerotic tissue. In the small thin stroma a large single perithecium may form, but generally there is a more or less continuous single layer of isolated perithecia produced so as to form a slight arc with the greatest depth at the center. Those at the center appear to be more advanced in the early development than those nearer the outer boundaries. The walls become sclerotic in nature and blue-black in color. The outer surrounding tissue is resistant, while the inner is more plastic and, on desiccation, separates from the more resistant wall. The

perithecia are variable in size and shape, but generally they are the shape of an Erlenmeyer flask, being broader at the base and gradually tapering toward the neck and mouth. In height they may measure 1240 microns, including the neck, which measures 138 microns. The base of the perithecium is about 320 microns in width, altho there is a great variation is sizes. The center of the perithecium shows the first indication of internal development by a slight clearing and breaking down of the cells. Later this cavity and the neck of the perithecium are filled with elongated cells resembling paraphyses which point toward the mouth of the neck. These cells appear to disintegrate partly and later give rise to the paraphyses and asci which can be observed with the unaided eye as an opaque mass of jelly. All of the asci are not formed at the same time, for asci of different ages may be found in the same perithecium. Even in perithecia that have partly discharged their ascospores the previous autumn, one may find new asci formed in the following spring.

The cylindrical, obtuse asci, that gradually taper at the base, measure from 110 to 180 by 10 to 13 microns, averaging 160 by 13 microns. The filiform, non-septate paraphyses show the greatest degree of variation, being from 120 to 320 microns or more in length. They may be 4.5 microns at the base and gradually taper to about 0.8 micron. Oil globules are irregularly distributed in the broader basal portion. There are typically 8 ascospores altho sometimes 6 are found in the ascus.

The ascospores are in a single row, ovate to globose, one-celled, at first hyalin, then opaque, and finally black with a depressed lighter zone or band extending about one-half of the circumference of the spore. Thru this depression the germ tube emerges and in the very old ascospores the depression is less readily observed. The ascospores formed on young apple trees inoculated with strains isolated from apple and mountain ash showed the average of 50 measurements to be 11.23 by 13.14 and 10.4 by 13.65 microns, respectively. The range in the former case was from 10.3 to 12.6 by 12.6 to 13.4 microns, and in the latter case from 10.3 to 11.1 by 12.6 to 14.2 microns.

At the time the asci are produced there is formed, in the region of the opening of the mouths of the perithecia, a layer of more or less coalescing groups of lighter-colored, thin-walled cells. This

layer of tissue acts as an abscission layer and, by the pressure from within the perithecium, the outer conidiophore cushion is sloughed away as a thin leathery sheath 0.5 mm. thick. It can sometimes be seen slightly raised from its previous position or it may be swaying in the wind from the margin of the old bark. This cushion, if not removed, as is often the case in the apple, prevents the discharge of the ascospores which are formed within the perithecium. Its removal exposes a blue-white to gray surface upon which the black ascospores may be readily observed. It appears that the perithecium, in taking up water, causes a swelling of the ascus; and that the cytoplasm of the ascus, together with that of some of the surrounding tissue, forms a mass of jelly-like substance which cements the discharge ascospores together to form a frass-like mass on the surface of the stroma.

Fig. 7.— Portion of a Stroma Showing Arrangement of Perithecia.

Figure 7 is a camera lucida drawing of a section 3.5 mm. high of a concave stroma as found on the apple. The conidiophore cushion, has sloughed away and the dark sclerotic boundary can be seen on the sides and continuing as a surface covering of the wood. In very old stroma the outer sclerotic tissue just beneath the perithecia may separate from the tan bark beneath and leave a deep, cup-shaped, sterile structure. (See Plate XII, *C*.)

It appears that in the formation and production of the stroma, the presence of the bark is necessary to make the structure complete. In its absence, the fungus produces a stroma composed of a mass of fleshy mycelium that becomes sclerotic and resembles that formed in artificial cultures. Stromata may also form at the end of a pruning stub or they may overrun the surface of older stromata, producing conidiophores and conidia in abundance, but in no case were perithecia formed.

The stromata are not formed to the same extent each year nor do all lesions produce them during the same season. They may form anywhere on the exposed tree and their development depends upon the available moisture rather than on sunlight or thickness of the bark. They may form from the middle of June until the middle

of September and are generally produced in the current season and less commonly in the bark killed the previous year. The thickness of the bark does not hinder their formation, altho slight differences can be observed when they are formed in thin and thick bark. Stromata are more numerous where the bark is gradually killed in the early summer than in the large areas suddenly killed as in the case of yellow streak. The formation of the perithecia on apple is the exception rather than the rule under New York conditions. This may be attributed to the abundant, well-distributed rains that prolong the radial growth so that the stromata are not formed until September. Further development of the stromata may be arrested by lack of moisture but, if favorably located, as on the lower side of a horizontal branch or near the border of the canker, they may receive and retain moisture from the rains and wood. As the spring of 1915 was favorable for stromata development, it was also favorable for the formation of perithecia in the older stromata. The asci may mature in stromata formed in a lesion produced earlier in the year, but generally two years or more are required for their maturity.

ASCOSPORE DISCHARGE

The logical period of spore discharge is in the autumn. Spores lodging upon a wound could then invade the tissue during the warm weather and produce a lesion the following spring. If disseminated in the spring the temperature is unfavorable for growth so that the fungus is unable to obtain a sufficient foothold before it is occluded by the radial growth. In 1915, when conditions favored the growth of the fungus rather than the host, the ascospores began to be discharged from the mountain ash on August 19, and in September and October the frass-like heaps of ascospores were common on the stromata on the apple as well.

GERMINATION OF SPORES

Mycelium may form from chlamydospores produced in cultures or in thick-walled sclerotic mycelium in the wood and stroma. Newly formed conidia, when placed in water, germinate by producing a germ tube 1 to 6 times the length of the conidium. The tube emerges at any place on the spore as shown in the camera lucida drawings in Fig. 8. Occasionally, two hyphal threads may be produced. Conidia taken from 20-day-old cultures and placed in water showed from

2 to 20 per cent germination. Within 20 minutes the tubes were 2 microns long and at the end of an hour, 3.5 microns in length. After that time no further growth was observvd. It was found that by placing a section of apple wood in a drop of water the percentage of germination was increased, and that the hyphal thread would continue its growth. The conidia from the cankers seldom germinate, but on cankered wood placed in a damp chamber for from 6 to 7 days, new conidia are formed. These conidia are viable and grow into long threads if placed in a drop of water containing a section of wood.

The ascospores, upon germinating, send forth one or two hyphal threads which emerge from the depressed, lighter region of the spore. When three threads are formed the third is generally a branch of one of the other two. A long, non-septate, unbranched, hyphal

Fig. 8.— Germinating Conidia of *N. discreta*.

thread is usually produced, but in some cases it becomes septate as shown in Plate XV, *C*. Very old ascospores, which have been retained within the perithecium for several years, when placed in distilled water or sugar solution may rupture the wall without any tendency to germinate.

On October 8, 1915, ascospores taken from the surface of a stroma were placed in distilled and tap water and the germination noted as from 1 to 3 per cent. When placed in a drop of water containing sections of green apple wood the germination increased to from 90 to 100 per cent. When placed in tannic acid (0.1 gram in 100 cc. water), lactic acid (0.3 per cent), or cane sugar (0.1 to 10 per cent), the germination was about the same as in distilled water. In cane sugar of greater density than 3 per cent, the hyphal thread becomes septate. Some investigators have observed the formation of conidia on the hyphal thread soon after germination, but this condition appears to be the exception rather than the rule.

The presence of sections of wood stimulated growth in the proportion of 1 to 10. Sections from the duramen showed as high a germination, but the mycelium was less vigorous than when sap wood was used. When the germination tests were made in vials, it was found that those spores in contact with the wood sections germinated more readily than those which were unattached.

On April 12, 1916, ascospores from the same tree as those utilized in the preceding experiment were again tested. The spores were exposed on the stromata on the north side of the tree thruout the entire winter. Some germination had occurred in the spore mass, but when tested in water the germination was found to be low. In this test, the ascospores were sown in distilled water on glass slides with or without the addition of sections of wood. The percentage of germination and the rapidity of growth after 24 hours are recorded in Table 2.

TABLE 2.— RAPIDITY OF GROWTH AND PERCENTAGE OF GERMINATION OF ASCOSPORES SOWN UNDER VARIOUS CONDITIONS.

MEDIUM	LENGTH OF HYPHAL THREAD	GERMINATION
	Microns	*Per cent*
Distilled water	10–30	1
Distilled water + Sections of apple wood dried at 110° C.	97–138	100
Distilled water + Sections of green apple wood	195–368	100
Distilled water + Decoction of green apple wood	138	100
Distilled water + Decoction of green apple wood boiled	179	100
Distilled water + Sections of oak board	16–22	100
Distilled water + Sections of dry willow branch	97–139	100
Distilled water + Sections of hemlock board	40–160	50
Distilled water + Sections of pine board	10–12	25

These results show that the stimulating effect of the presence of the sections of wood is not due to any enzym that may be present in the wood, but rather to an increased food supply.

DISSEMINATION OF SPORES

In a young apple orchard, trees situated near an old tree or near a woodlot are more diseased than those further removed, indicating that distance from the source of infection is a means of protection.

It is evident that there are several possible agencies by means of which the fungus may be disseminated, but it is difficult to obtain data that will fix the responsibility. Such agencies as man, insects, rain, and wind appear to be the most important means of distribution.

INSECTS

Insects have been shown by the writer (12) to be carriers and disseminators of fungous spores. It was found that the tree cricket may eat the ascospores of *N. discreta* without impairing their vitality by the intestinal juices in the digestive process. The female insect, after ovipositing in the bark, seals the opening made with a pellet of excrement that may contain fungus spores, thus duplicating somewhat the methods used in artificial inoculations. In New York, the blister canker is seldom formed about such punctures. It is possible that the insect in ovipositing does not penetrate the wood and thus permit the fungus to obtain a proper foothold. However, a more plausible explanation may be the lack of ascospores which are produced only under the most favorable conditions. Therefore, while insects such as the tree cricket may be carriers of the fungous spores, they can hardly be considered as active agents under New York conditions.

RAIN

It is apparent that during a rain the ascospores on the surface of a stroma would, in time, be carried away. It was deemed of interest to see how many spores were carried downward by the rain, so spore traps made from glass slides and cotton as described by Heald and Gardener (15) were placed beneath cankers in the direct line of streams of water which drained from the branches.

Since only those cankers which showed ascospores on the surface of the stromata would give results, it was necessary to determine first the presence of such spores. As has been pointed out, where the conidiophore cushion was still present the mature ascospores may not discharge. Hence, a mountain ash 9 meters high was selected which at from 2 to 2.6 meters above the ground, was dotted with stromata. The ascospores on the stromata situated on the south and southwest sides of the tree were present only in thin layers as most of them had been washed away. On the other sides of the tree, the spores were in heaps 5 mm. deep. Counts made by a

hemacytometer showed that from 3 to 5 million ascospores may be present in the frass-like heaps. Nine traps were placed in favorable locations, and on October 30, 1915, there was 0.23 inch of rain driven slightly by a west wind. The cotton of the traps, except those on the east side, was wet.

The cotton from each trap was agitated in distilled water several times and the final liquid made up to 50 cc. The average of 5 hemacytometer counts made from the various agitated liquids showed the following number of spores: South side, 144,000; southeast side, 250,000; east side 466,000 and 877,000; northeast side, 933,000 and 1,866,000; northwest side, 833,000 and 1,944,000; and at the base of the east branch, 511,000. It should be noted that the spores caught by the east traps may have been dislodged from the stromata by agents other than rain. These counts are only relative, for many of the spores were enmeshed in the cotton and would not separate out even after long agitation. From these data, it is estimated that 17 million spores were washed down the trunk which is the number found on 4 or 5 stromata.

The figures given above apparently are too low considering the large number of spores present. Hence a branch of the mountain ash 28 cm. long and 4.5 cm. in diameter, with 88 stromata having at least 350 million ascospores on their surfaces, was attached to the bottom side of a tin can. The can was perforated in such a manner that a uniform amount of water flowed over the surface of the branch at the rate of 360 cc. per minute for 5 minutes. The water was collected by means of a funnel and the spores filtered out by placing cotton at the end of the funnel. Hemacytometer counts of two tests showed 566,466 and 333,000 spores, respectively. Two days later the experiment was repeated when 1,155,000 and 283,000 spores were counted. On October 14, 1915, rain being predicted, the experiment was set up in the open without the tin can. After a slow continuous rain of 0.96 inch, 633,000 spores were collected. This was repeated October 30, with 0.23 inch of rain and 222,000 spores collected.

An examination of the stromata on a mountain ash branch (Plate XII, *A*) will show the structure of the periderm that prevents too rapid a distribution of the spores. The running water is deflected by the stellar openings in the periderm about the stroma, and in

the case of a strong flow, such as is encountered by placing the branch under the faucet, an air cushion is formed between the water and the spores. In the earlier stages, when the hygroscopic mycelium at the base of the curled back periderm opens and partly closes the stellar opening, this effect is more pronounced.

The orchardist, noting these bewildering figures may wonder how there is a healthy apple tree left. While, potentially, each spore, under favorable conditions, is capable of producing a canker, there are few spores that ever function in that capacity. On April 15, 1916, during a light rain 2 to 3 cc. of liquid, containing 130,000 viable ascospores per cubic centimeter, was sprayed by means of a painter's atomizer upon 24 apple wounds. The wounds were made in February on 18-and 40-year-old trees and showed the usual amount of checking. In cases where spore masses were sprayed on the cut surfaces they were crushed and rubbed into the cracks. Later in the season some of the pruning wounds showed slime flux, but it was not until 1917 that one of the treated wounds produced a canker. The presence of a pruning wound several centimeters above prevented a rapid healing of the wound and thus the thin callus which was formed was readily killed by the fungus. In 1918 this canker enlarged and formed a canker 15 cm. long. It is possible that, had this experiment been performed in the autumn, the fungus would have had a longer period in which to become established before being occluded by the radial growth.

WIND

Attempts were made to determine the number of ascospores which might be transported by the wind. Petri dishes containing nutrient glucose agar were exposed from 1 to 10 minutes at from 5 to 15 paces from the mountain ash described above. The dishes were placed in direct line with the prevailing wind and when examined under the microscope no ascospores were found, tho but a short distance away there were millions of spores ready to be disseminated. The spores were in masses, however, which would disintegrate only in the presence of water. Wolf (37) found the spores of this fungus twice in 27 exposures, and McCubbin's experiments (20) indicate that the dry spores are capable of being transported miles.

PATHOGENICITY

Attempts were made to induce canker formation by placing mycelium upon the uninjured bark. Small glass cylinders were attached to the bark and the mycelium and substratum placed in the chamber which was sealed to prevent drying and contamination. Germinating ascospores were sprayed upon the foliage of young trees growing in the greenhouse and such trees or branches were placed in a damp chamber. Mature as well as growing green fruit were inoculated, the latter healing and producing an abundance of stone cells in the injured tissue. In all these special tests the results were negative and it appears that the fungus is only a wound parasite.

METHOD OF INOCULATION

At the outset of the experimental work wounds were made by means of a scalpel or by drilling a hole 1.3 cm. deep into the branch so as to penetrate to the wood. The hole was then capped with a sterile cork and covered with grafting wax. Such wounds had many objections and, finally, a carpenter's automatic spring-drill was used with success. A 1-mm. drill was used on the small twigs, while a 3-mm. drill gave the best results on the larger branches. The usual precautions were observed in sterilizing the branches, instruments, etc. Mercury bichloride (2 parts to 1000 of water) was used to sterilize the surface of the branches, while the instruments were placed in 95 per cent alcohol and flamed just prior to using.

The actively growing mycelium from pure cultures of *N. discreta* was inserted into the sterile chambers, together with some of the substratum of moist bread, oat meal agar, potato starch agar, or nutrient glucose agar. The fungus was thus enabled to continue its growth on the culture medium until the mycelium could establish itself in the wood. It was observed that excess water from the moist substratum was readily taken up by the suction within the wood. The chambers were covered with warm grafting wax in order to avoid desiccation or contamination.

Altho it may appear that needless pains were taken in covering the wound, such is deemed necessary in view of the long interval that may elapse between the time of inoculation and the formation of the canker. Some maintain that an active parasite ought to

attack the host immediately after the mycelium is inserted, but it is evident that such an impression is erroneous and that our conception of parasitism must be altered. After the canker had formed and the bark was more or less cracked, the wax covering was of secondary importance. The writer was able to use the same wax thruout the year by covering the pellet with a coat of orange shellac, thus preventing it from running on hot days and from sloughing off in cold weather, due to the swaying of the branches.

INOCULATIONS

Inoculations were made on apple, pear, mountain ash, elm, hawthorn, plum, peach, white birch, and Judas tree (*Cercis canadensis*), but only those on the first three hosts were successful. The inoculations were made under varying conditions, the most important of which were as follows: (1) Apple trees of various ages growing in the field or greenhouse were inoculated at different periods of the year with strains isolated from apple or mountain ash. (2) Inoculations were made on 3-year-old Ben Davis trees grown in the greenhouse, some with a limited and others with an ample supply of water. (3) Branches of varying ages on the same tree and slow and rapidly growing branches of the same age on the same tree were inoculated. (4) Badly cankered trees were inoculated to determine if cankers would form more readily on such trees. (5) Partially or totally frozen trees, artificially defoliated trees, and girdled trees were inoculated. (6) Branches just beneath an uncovered pruning wound were inoculated, while others were covered with coal tar, shellac, paint, shellac plus paint, and shellac plus tar. (7) Well-sealed inoculations were compared with those having free access to the air by means of crooked, sterile, glass tubes whose opening contained a cotton filter.

Table 3 contains a summary of all of the inoculations. In all cases one check was made for every two inoculations and as the checks remained sterile they are not included in the table.

Table 3.— Results of Inoculations with *N. discreta* on Apple and Other Hosts.

Date of inoculation	Host	Age of host, years	Total number of inoculations	Inoculation notes	Number of cankers formed	Results
				1912		
May 21	Henderson Sweet	40	15	Scalpel and auger wounds	9	Cankers small, formed 1912
June 19	Henderson Sweet	40	9	Scalpel wound	1	Sap exuded 1914
June 19	Red Astrachan	40	7	Tree badly cankered	2	1 canker 1913 was 13 cm.
June 20	Northern Spy	40	6	Stubs	0	Sap exudate
June 20	Northern Spy	40	10	Scalpel and auger wound	2	Sap exudate
July 3	Northern Spy	40	15	Suckers	0	Sap exudate
July 31	Henderson Sweet	40	1	Branch girdled	0	Dead April, 1914
July 31	Henderson Sweet	40	9	Stubs	0	
Aug. 1	Northern Spy	40	1	Girdled branch	1	Healthy June 1914; stromata 1918
Aug. 1	Northern Spy	40	1	Below girdle	0	
Aug. 1	Northern Spy	40	6	Auger wound	0	
				1913		
June 6	Henderson Sweet	41	10	Scalpel and auger wound	1	Canker small
June 6	Red Astrachan	41	2	Tree badly diseased	0	
June 6	Northern Spy	41	6	Scalpel	0	Edematous about incision
June 11	Northern Spy	41	4	Auger	0	Edematous about incision
July 1	Northern Spy	41	6	Scalpel	0	
July 1	Northern Spy	41	1	Girdled branch	1	Canker 20 cm. in 1918
Aug. 19	Red Astrachan	41	5	Auger and scalpel wound	2	Canker 14 cm. in 1914
Aug. 19	Henderson Sweet	41	8	Auger and scalpel wound	0	
Aug. 21	Henderson Sweet	41	11	Auger and scalpel wound	0	
				1914		
Mar. 16	Hanlon	18	6	Stubs	3	Cankers edematous
Apr. 17	Baldwin	25	7	Stubs	2	In 1918 cankers 23–30 cm.
Apr. 17	Rome Beauty	2	5	Greenhouse	0	
May 26	Hanlon	18	7	Stubs	0	
June 5	North Western Greening	30	10	Stubs	0	
June 6	North Western Greening	30	4	Stubs	0	

TABLE 3.— RESULTS OF INOCULATIONS WITH *N. discreta* ON APPLE AND OTHER HOSTS (*continued*).

Date of Inoculation	Host	Age of host, years	Total number of inoculations	Inoculation notes	Number of cankers formed	Results
				1914		
June 6	North Western Greening	30	1	Girdled branch	0	Broken off, 1915
June 10	North Western Greening	30	2	Stubs	0	
July 16	North Western Greening	2	4	Frozen, greenhouse	0	
July 17	North Western Greening	30	4	Stubs	0	
July 21	Baldwin	40	18	Stubs and branches	0	
July 29	Montgomery	2	16	Greenhouse	3	Cankered 1915
July 31	Northern Spy	41	36	Stubs and branches	0	
Aug. 25	Rockland	2	6	On trunks	3	Cankered 1916
Aug. 25	Herkimer	2	4	On trunks	2	Cankered 1916
Oct. 9	Baldwin	25	10	Stubs and branches	1	Yellow streak 1917
				1915		
Mar 27	Montgomery	3	8	Greenhouse	2	Killed Oct. 1915
Apr. 24	Rockland	3	6	In orchard	2	Cankered May 1918, stromata
Apr. 24	Herkimer	3	6	In orchard	0	
Apr. 26	Northern Spy	42	48	Stubs and branches	4	Stromata 1918
May 4	Winter Citron	18	4	Before freezing	0	
May 4	Rioter	18	5	Before freezing	0	
May 10	Baldwin	25	7	Partly frozen May 14	1	Yellow streak 1917
May 10	Northern Spy	42	6	Carpenter's drill used	0	
May 11	Northern Spy	42	34	Stubs and branches	1	Staghead and yellow streak 1918
May 12	Northern Spy	42	18	Stubs and branches	0	
May 15	North Western Greening	3	2	Greenhouse	2	Trees killed, stromata
May 23	Rioter	18	5	Tree frozen	0	Black heart formed, not killed
May 26	Winter Citron	18	3	Tree frozen	0	Black heart formed, killed
May 27	Montgomery	3	12	Greenhouse	0	
May 28	Rockland	3	4	In orchard	0	
May 28	Tioga	3	9		0	

May 28	Herkimer	3	6		2	Cankers small
June 3	Northern Spy	43	8	Stubs and branches	0	
June 3	North Western Greening	43	13	Stubs and branches	0	
June 4	North Western Greening	43	18	Stubs and branches	0	
July 15	Baldwin	43	14	Stubs	5	Cankers 7–40 cm. in 1918
Sept. 15	Baldwin	43	50	Branches	3	One yellow streak 1918
Sept. 16	Baldwin	43	20	Scalpel, new strain	2	Cankers 12 cm. in 1918
Sept. 16	Baldwin	43	20	Drill, suckers, new strain	19	Some healed after cankers formed
Sept. 16	Baldwin	43	8	Branches	7	Cankers 5–15 cm. May 1916
Sept. 17	Baldwin	43	30	Stubs	17	Some formed 1917, others 1918
Sept. 29	Baldwin	43	10	Scalpel	5	Cankers 1–2 cm. May 1916
Sept. 30	Baldwin	43	20	Scalpel	5	Cankers 1–2 cm. May 1916
Oct. 18	Baldwin	43	23	Drill	20	Cankers 1–9 cm. May 1916
Oct. 20	Baldwin	43	18	Drill	17	Cankers increased 1917–18
Oct. 26	Baldwin	43	24	Stubs	20	Cankers formed stromata 1918
Oct. 27	Baldwin	43	28	Stubs	15	Cankers formed stromata 1918
				1916		
Jan. 5	Ben Davis	3	2	Greenhouse	2	Killed, stromata
Jan. 5	Seedling	4	10	Greenhouse	8	Killed, stromata
Jan. 21	Rockland	5	20	In orchard	8	Island cankers June 1917
Jan. 21	Herkimer	5	19	In orchard	2	Cankers formed May 1917
Mar. 25	Baldwin	44	20	Stubs and branches	5	1 branch killed
Apr. 3	Baldwin	44	4	Stubs and branches	2	Bark edematous
Apr. 20	Ben Davis	3	23	Greenhouse	23	Killed, stromata
Apr. 20	Mountain Ash	3	4	Greenhouse	4	Killed, stromata
Apr. 28	Pear	20	13		5	Edematous, formed May 24, 1916
May 11	Baldwin	44	10	Mountain Ash strain mycelium	5	Stromata 1918
June 5	Montgomery	4	2	In greenhouse	0	
June 22	Northern Spy	44	6	Branches	6	Cankers 15 cm. in 1918
June 22	Baldwin	44	12	Branches	12	Cankers 1–4 cm. in 1916
July 31	Baldwin	44	18	Branches	5	Healed later
Aug. 4	Ben Davis	3	6	Greenhouse	4	Cankers 2.5–4 cm.
Aug. 4	Ben Davis	3	8	Greenhouse, defoliated	6	Island cankers 48 cm. from inoculation
Aug. 4	Mountain Ash	4	1	Greenhouse, defoliated	1	Killed
Aug. 7	Westchester	5	8	In orchard	1	Canker formed May 1917, 30 cm.

TABLE 3.— RESULTS OF INOCULATIONS WITH *N. discreta* ON APPLE AND OTHER HOSTS (*concluded*).

Date of inocu-lation	Host	Age of host, years	Total number of inocu-lations	Inoculation notes	Number of cankers formed	Results
				1916		
Aug. 7	Clinton	5	6		0	
Aug. 10	Northern Spy	25	10		5	Exudation of sap
Aug. 24	Northern Spy	25	10	Tree defoliated	2	
Aug. 24	Baldwin	44			0	
Sept. 15	Baldwin	44	22		4	Sap exudate
Sept. 27	Baldwin	44	18		15	
Oct. 2	White Birch	20	6	Tree bleeding	0	
Oct. 2	Elm	50	4		0	One shows slime flux
Oct. 2	Elm	10	6		0	
				1917		
Mar. 22	Baldwin	46	10	Stubs and branches	3	Yellow streak 115 cm. in 1918
Mar. 22	Baldwin	46	6	Suckers	0	
Mar. 22	Northern Spy	25	6	Defoliated 1916	3	Cankers formed 1918
Mar. 22	Baldwin	46	4		0	
Apr. 4	Pear	21	20	Leaf buds 2 cm.	14	Edematous May 3
Apr. 4	Pear	21	18	1 year shoots	12	Formed at closed cluster bud stage
Apr. 28	Baldwin	46	6	Old branches	4	Formed, 1917; enlarged, 1918
Apr. 28	Baldwin	46	9	1–2–3-year branches	9	Formed closed cluster bud stage
Apr. 28	Baldwin	46	9	1–2–3-year suckers	9	Formed closed cluster bud stage
Apr. 28	Ben Davis	4	14	Leaf buds opening	13	
Total	......	......	1,144		374	
Checks	......	......	583		0	

SUMMARY OF OBSERVATIONS

Space does not permit a detailed account of the history of the individual cankers. However, as environment plays an important rôle, it is necessary to include in this brief summary a discussion of the effect of the weather conditions upon the inoculations as well as upon the natural cankers.

Observations for 1912.— The rains of May, amounting to 7.2 inches, stimulated radial growth to such a degree as to result in the formation of growth fissures. In some cases the cracked bark exposed 1 cm. of the underlying wood which callused over as the season progressed. Slime flux or an abundance of sap flow was common from diseased pruning wounds. Cankers enlarged from June 25 to July 15, and but few branches showed staghead during this drier period. Bark about the margins of the cankers became edematous from July 22 to 29, and by September a few stromata were in evidence. On November 10, yellow streak was forming about the proximal end of the cankers, and, during the moderate weather up to December 19, the cankers enlarged. Also, during the heavy May rains, the inoculations showed a copious flow of sap which was more or less persistent until 1916.

Cankers formed about the inoculations on July 7 and July 23, and the bark about some of the inoculations became edematous even tho no canker formed. In some cases where a large impervious covering or wax pellet was placed over the abrasion, superficial areas of dead brown bark were formed about the inoculations as well as on some checks. These areas were the size of the covering and it appears that they were due to the exclusion of oxygen from the exceptionally active bark by the impervious covering. They were readily distinguished, for in the true canker the dead bark extended to the wood and was not superficial.

Observations for 1913.— The first half of May was devoid of rain and the natural cankers began to enlarge the last week in May, a month earlier than in 1912. This activity was checked by the rain of June 1 (1.27 inches), which stimulated radial growth and slime flux. The rain of June 26 produced an edematous condition of the bark and stromata were formed by July 3. The cankers gradually spread in the warm months forming dark brown dead bark and the rain of August 29 (1.12 inches) resulted in a sudden spread of yellow streak which was observable September 15.

Some of the inoculations made in 1912 produced cankers in the spring at the time the trees were in bloom. Inoculations made June 10, showed edematous bark without canker formation. Most of the inoculations were made too late in the season to produce cankers and it became evident that infection did not take place at all times of the year.

Observations for 1914.— The rains of May (4 inches) and August (6.05 inches) saturated the soil to such a degree that the light, well-distributed rains during the other months were sufficient to maintain a vigorous growth of the host. This shows that the total yearly rainfall may result in misinterpretation of data if considered irrespective of its distribution. The cankers enlarged about June 1, and stromata formed July 1, none forming later. There was a slight enlargement of the cankers in August and also from October 27 to December 15.

The inoculations made March 16 were the only ones that formed cankers by May 26, and the year, as a whole, resembled 1912.

Observations for 1915.— The rains of March (0.65 inch), April (0.64 inch), and May (2.41 inches), when considered in connection with the subnormal precipitation of the latter quarter of 1914, resulted in a low water level in the soil. The warm period from May 26 to June 15, which includes the blooming period, was also devoid of rain. This had a notable influence upon the trees for at the proximal ends of pruning wounds V-shaped areas of dead bark, ranging from 2 to 20 cm. in length, formed about both treated and untreated wounds. Some were due to the fungus *N. discreta* while others were the result of desiccation. On June 1 dying branches could be observed, which in other years would not be seen until the dry weather of July. Old and newly formed cankers enlarged, and by June 24 stromata were formed. On August 12, newly formed asci were found in the stromata of 1914 formation. The rains of August (5.9 inches) checked the advancing margins only temporarily for, during the warm dry month of September (1.78 inches rainfall), they were again active. At that time asci were found in stromata formed earlier in the season, and, toward the end of the month, ascospores were found heaped on the surface of the stromata of the apple and mountain ash. Such an abundance of ascospores was not observed at any other time during this study.

The inoculations were not very successful due to the fact that they were made mostly upon Northern Spy which was the only variety then available, and which was subsequently found to be quite resistant. Inoculations made in the autumn were more successful because, for the most part, they were made on the Baldwin. Also, by comparison, it was later found that the strain heretofore used had become devitalized and had lost its ability to invade the bark and produce a canker, altho able to invade the wood. The use of a carpenter's automatic spring drill was also found to be more satisfactory than the incisions made with a scalpel.

Observations for 1916.— The rainfall in the spring was so excessive that farmers had difficulty in plowing their land until the last week in May. The heavy rains ceased the latter part of June, and following the drier month of August a few cankers enlarged in September with slight stromata formation. The rain of September 8 stimulated the apical growth of the twigs and edematous yellow streak was formed about September 16. In the latter part of November, after the leaves had fallen, some of the cankers showed the formation of yellow streak.

The development of cankers about inoculations was common from the beginning of cambium activity until after the petals fell in spite of the heavy rainfall. Inoculations made in previous years, and which had been quiescent, showed canker formation at that time. It became evident that cankers developing from inoculations were influenced by factors not involved in the formation of the natural cankers.

Observations for 1917.— The year was similar to the previous one in that there was an excessive rainfall during the growing season which had been delayed three to four weeks at the outset by cold damp weather. A few cankers advanced their margins in the spring but were arrested at the time of blooming, May 29. The usual formation of new cankers did not take place in June, altho there was a slight enlargement of the old ones in the latter part of August. On October 21, before the leaves had been shed (tho some were turning yellow), the formation of yellow streak was observed.

On May 14, cankers began to form about inoculations while the flower buds were in the closed cluster stage. In cankers which had formed in previous years and which had produced a callus, the callus had been killed with a result similar to that observed in the European canker.

Observations for 1918 and 1919.— These years were a mere repetition of the foregoing. The old inoculations gradually spread their margins and each year the canker spread more rapidly than the year before. In 1919, some of these cankers were over 2 meters in length with no doubt as to the cause of the disease for stromata were abundantly formed.

DISCUSSION OF THE INOCULATIONS

Before one can discuss the results of the inoculations a clear conception must be had as to what actually constitutes a successful inoculation. The question arises as to whether or not only such cases as produce cankers should be considered successful. Such a classification, however, would be one-sided for it would overlook the ability of the fungus to penetrate the woody tissue as a parasite without the formation of a canker. Thus it is evident that the fungus must be considered in the light of a parasite on the wood as well as on the bark.

In all of the inoculations examined, the formation of the dark brown, water-logged streaks from 8 to 100 cm. long could be traced in the woody tissue. These varied in size from a mere dot composed of a group of discolored cells up to areas the size of the cross section of an entire branch. (See Plates VI, *B;* VII, *B*, *C*, and *D*; IX; X, *A*; and XIII, *C*.) The streaks developed best in the outer annual ring even tho the mycelium had an opportunity to penetrate into the older wood. Such streaks should not be confused with those lighter, smaller discolorations which are produced in the checks as the result of oxidation and desiccation. Generally the formation of the streak preceded the infection of the bark, but it may be independent of bark infection. In the spring the streaks appear slightly earlier than the advance of the margin of the lesion in the bark, but as the season advances this relation does not persist for the streak may continue to penetrate into the wood.

While the fungus can be considered as producing 100 per cent infection in the wood, as a parasite of the bark the percentage of resulting cankers is variable. Also, those varieties resistant to bark infection may not be resistant to wood infection. Since the external appearance of infection is more readily observed, this phase of parasitism is the one usually considered. A canker was regarded as having been formed when a definite area of bark was killed to the

wood. Such a lesion might continue its development as a canker or it may be delimited by a callus, which in turn may be killed later.

The following conclusions have been reached after observing the behavior of the cankers resulting from inoculations:

1. Inoculations result in cankers if made from September up to the time the buds are expanding. When inoculations were made from June 1 until September, cankers seldom formed under New York conditions. The period of the greatest manifestation of infection, resulting in canker formation, extends from the awakening of the cambium until radial growth becomes rapid enough to occlude the mycelium. This stage usually terminates at the time the petals fall, but may extend into June or even July in periods of drought.

2. Considering the interval from the time of inoculation to the formation of a canker as the period of incubation, this period may extend from less than 2 days to 9 months or more. If the inoculation is made in the spring only a few days will elapse before a canker is formed, while inoculations made in September will also result in the formation of a canker in the spring.

3. In the period of greatest manifestation of artificial inoculation heavy rains had no apparent influence in preventing the formation of cankers. After artificial cankers have become established they behave the same as natural cankers, and are then influenced by the heavy spring rains which stimulate radial growth. Slime flux, or the excessive bleeding from an inoculation, may result even tho no bark infection may be observed. Trees grown in the greenhouse and sparingly watered so as to maintain a low soil moisture content were compared with those supplied with ample water. It was found that smaller cankers developed on the trees receiving a limited amount of water. Finally, it became necessary to water the trees in the dry plat, and 20 days later yellow streak from 5 to 100 cm. in length formed in place of the intermittent patches of brown, discolored, or island cankers which formed for a similar distance on the trees receiving ample water. Altho the temperature of the greenhouse was favorable for canker development none was manifested until the buds began to push forth.

4. Due to the earlier cambium activity of the pear, cankers are formed earlier in the spring than on the apple altho in both cases the cankers are formed at the same stage of growth.

5. Inoculations made on lateral branches of the same tree at places not in the direct line of sap flow, will form the latest cankers of the season. If seedling suckers coming from the roots are inoculated, they may form cankers later in the season than those made on the grafted tree top, due to difference in cambium activity.

6. The presence of mycelium in the wood has an inhibitory influence upon radial growth even tho no external bark infection is observed. Inoculations may not form cankers the first year but the mycelium may invade the wood for several years before a canker is finally formed. Cankers may not form about the abrasion but may have their centers some distance away.

7. Inoculations made about treated and untreated pruning wounds produced cankers to the same degree, as the covering had no influence on the size of the canker formed in the spring of the year, altho according to Münch (22) larger cankers should have been formed where the tissues had been desiccated. Stromata formed readily about pruning wounds, while in the case of an enclosed type of canker they were rare or never produced.

8. Attempts to stimulate the processes involved in the shedding and the production of leaves by means of artificial defoliation of trees in the greenhouse or orchard showed no influence upon canker formation.

9. The total or partial artificial freezing of trees in the late spring did not induce canker formation. It is possible that a tree may have its growth impaired by low temperature so as to enable the fungus to produce cankers, but such a condition then becomes contributary rather than primary.

10. Inoculations made on badly cankered branches or trees from June to September did not produce cankers, altho at the same time the natural cankers were enlarging their margins. Inoculations made at the same time on girdled branches also failed to produce cankers.

TAXONOMY

In the literature, many species of Nummularia are recorded on various hosts. Some of these species are distinguished only by slight differences of form or structure and no doubt are identical. It is to be expected that *N. discreta* would show different growth characteristics on artificial media, and that variations in the structure of the wood and bark, and in food storage of different hosts would

influence the formation of the stromata. The interrelation of the various species, however, can only be determined by cross inoculations.

The synonyms and the mycological literature of the descriptions are given below.

Nummularia discreta (Schw.) Tul. Tulasne, Sel. Fung. Carp. 2:45, pl. 5, fig. 1–10. 1863. Nitschke, Pyr. Germ. 67, 1867. Fuckel, Sym. Myc. 236, 1869. Ellis and Everhart, N. Am. Pyr. 622, pl. 39, fig. 9–11. 1892. Jacsewski, Bul. Soc. Myc. Fr. 11: 108, 1895. Saccardo, Syl. Fung. 1: 398, 1882.

Sphaeria discreta Schw. Schweinitz, Trans. Am. Phil. Soc. 4: 195, no. 1249. 1834.

Sphaeria excavata Schw. Schweinitz, l. c. no. 1250. See Ellis and Everhart, N. Am. Pyr. 622, 1892.

Sphaeria discincola Schw. Currey, Trans. Linn. Soc. London 22:274, no. 106, pl. 47, fig. 105. 1858. Not considered the same as described by Schweinitz, Schr. Naturf. Ges. Leipzig 1: 34, no. 63, 1822 or Fries, Syst. Myc. 2:368, no. 97. 1822. Also see Schweinitz, l. c. no. 1249.

Sphaeria (Diatrype) discreta (Schw.) Rav. Ravenel, Exsicc. Fungi Car. 2: no. 57. 1853.

The description of *Nummularia rapanda* (Fr.) Nke., reported in Europe as occurring upon *Sorbus aucuparia*, resembles very closely that of *N. discreta*, differing only in the size and shape of the spores. The writer has examined herbarium specimens of the former organism, but has been unable to obtain fresh material from Europe for use in cultures or inoculations.

In 1914 and 1919 the writer observed an uncommon fruiting form of the fungus on the transverse cuts of pruning wounds and on stromata which were not attached to the wood. These stromatic cushions are similar to those formed in artificial cultures and develop when the bark is lacking. These bodies measure from 5 to 30 mm. in diameter and from 2.5 to 5 mm. thick, with conidia formed in abundance upon their surface.

PATHOLOGICAL HISTOLOGY

Macroscopically, it is noted that the invasion of the fungus is accompanied by definite changes in the wood and bark, both becoming discolored. In the case of the wood, it is at first dark in color while upon drying it assumes a lighter shade. The exposed surfaces become carbonaceous and the wood becomes heavier and is infiltrated with wound gum. In sawing a diseased dry branch, it is noted that the saw glides over the wood in a manner similar to that experienced in cutting a horny substance. In the mountain ash the bark parenchyma is readily disintegrated leaving the more resistant

periderm and fibers. The surface of the wood becomes carbonaceous and brittle, while the interior of the branch finally becomes pulpy and cream colored. Where the fungus has been present for many years, the summer wood of several annual rings may be of a blue-green color, and such tissue shows less delignification and disintegration than the spring wood of the same season. The disintegration is due to the disappearing of the middle lamella.

The microscopic changes in the apple can best be seen in the inoculations without discounting for the results produced by secondary fungi. When an incision is made by means of a carpenter's automatic spring drill, the woody tissues can be penetrated for several annual rings if desired. The conductive elements are thus ruptured and by oxidation and desiccation a light brown area of discolored tissue from 0.5 to 10 cm. long may be formed in the wood of the checks.

Streaks resulting from fungus invasion are readily distinguished from the checks as darker discoloration generally arises from the side of an abrasion tho less oftener it may be seen as a continuation of the dry triangular areas as noted in the checks. These are illustrated in Plate VII, *B* and *C*, and can be compared with the check *D*. It was also observed that the wood was discolored to the depth that the drill penetrated into the wood, yet the fungus made its greatest growth in the outer annual ring before radial growth took place. As the canker increases in age the last annual ring is generally invaded anew from the open cankered tissue near the source of infection. The largest number of streaks were formed in the year the inoculation was made. (See Plate IX, *D*.) The parallel streaks are independent and do not cross, altho they may coalesce to form irregular or fan-shaped discolored masses. (See Plate X, *A*.)

The streaks vary in length depending upon the variety of apple attacked, the environment, and the time of inoculation. As already stated, the formation of a streak does not necessarily mean the formation of a canker, nor is there any correlation between the length of the streak and the size of the canker that is formed. If inoculated in September, the streak may attain a length of 115 cm. and if inoculated in the spring it may be but slightly longer than the resultant canker. On a cankered branch 4.5 cm. in diameter the streak was a mere dot 70 cm. distant from the lesion. At 60 cm. this same streak measured 6.5 by 1 mm., and at 53 cm. it was 6.5

by 4 mm. At the border of the canker it attained a size of 4 by 2.2 cm., and extended to the center of the branch. At 30 cm. below the lesion there were 21 streaks present, which varied from a dot to 2.5 by 5 mm. in size, and which were present in the outer 3 annual rings. The presence of the streaks in the vicinity of the bark inhibits cambium activity, reduces the radial growth (Plate IX), and may form a groove in the outline of the trunk. This is significant, for in time there is produced an accumulative effect finally resulting in a radial growth so small that the fungus has but little tissue to invade before it attacks the bark. Hence, the spread of the margins of a canker along the axis of a branch appears to be accelerated as the canker increases in age (page 19), and its importance in any surgical treatment becomes self-evident.

The formation of the streaks and the discoloration at the center of a branch are not the same altho somewhat related. Due to the fact that they may be encountered upon the same branch, the duramen or heartwood, which is of a dark brown color, is often mistaken as a result of the blister canker. On the older branches the discoloration may be due to desiccation and oxidation, winter injury, or the result of fungus invasion. The degree of duramen formation depends upon soil moisture. Apple trees 25 years old grown on shallow soil with hardpan beneath may show the duramen from 3 to 4 cm. from the bark, while on heavier soils little duramen may be present. That the streaks of the blister canker are independent of the duramen was observed when 5-year old Ben Davis trees were inoculated and failed to show discoloration of the center of the trees after two years. (See Plate IX, *D.*) Inoculations made on branches where duramen is present show that the streaks are independent at first, but later the various stages of their union can be observed as forming one continuous irregular dark axil or center. For this reason, attempts to isolate the mycelium from such duramen have resulted in failure, but by the closet scrutiny, the presence of darker streaks can be traced in the discolored wood.

The penetration of the fungus into the living wood produces a rearrangement of the sap flow as the discolored streaks are surcharged with sap. A similar sap flow is observed from the duramen and is most copious after a protracted rain. This sap must either be transported by means of the cell walls, for the lumen of the conductive tissue is clogged with wound gum, or else transported radially

to the discolored tissue by the medullary rays. If a section of such a branch is taken into the laboratory, the sap flow may continue for some time even tho severed from the roots.

A close examination of the streak usually discloses an outer band of lighter colored, dryer wood than is normally found. At the extremity of the streak this lighter tissue occurs as a continuation of the dark streak. When examined under the microscope, the longitudinal sections of dot-like streaks shows the mycelium in the tracheal tubes. (See Plate XV, *B*.) The neighboring cells are discolored brown to wine red with less wound gum present in those cells furthest removed from the mycelial strand. The medullary rays that cross such a streak show the cells nearest the streak also as discolored, indicating that the discoloration is diffused slightly in a lateral direction as well as along the conductive elements. In one case, two streaks in the same annual ring were crossed by the same medullary ray while the intervening cells were not discolored. In the advancing margin the growth in the wood is mostly in the tracheal tubes with but little lateral growth. In the older diseased tissue, the mycelium can be traced in the wood parenchyma and fibers. Whether the fungus advances first and the discoloration follows later or vice versa, depends upon the time that the observation is made. Generally the discoloration is seen in advance of the mycelium but in many cases the mycelium has been found in the conductive elements in advance of any discoloration. Blue-green to black lines may form in the wood and upon examination are seen to consist of thick-walled mycelial cells or chlamydospores with more or less discoloration of the surrounding wood. This coloring, however, is more pronounced in the mountain ash than in the apple. The outer wood exposed to the air may become carbonaceous due to the interaction of sclerotic mycelium and the wood. Softer wood or bark that may lie above such resistant tissue soon weathers away.

BARK

The bark shows a distinct brown discoloration of the cells. The mycelium does not penetrate the bark in the same manner at different periods of the year when cankers enlarge. In the spring along the advancing margin the cambium is discolored, while the previous year's phloem shows discolored cells more or less irregularly distributed. The medullary rays and the older phloem parenchyma are

browned, while the other elements of the old phloem are non-colored thus forming tiers of non-colored cells surrounded by a rectangular border of colored tissue. The non-colored elements, however, disintegrate more readily and at rare intervals coalese forming a horizontal layer dividing the green bark in two parts separated by a mushy continuous layer of broken down cells. In some cases the fungus penetrates the outer bark more readily than the inner and thus the margin of the canker may have pronounced sloping sides which must not be mistaken for callus. This form of invasion is manifested late in the summer or early autumn.

There appear to be two distinct ways that the bark may be penetrated and these can be observed in the artificial inoculations and in the natural cankers. In the case of the inoculations, the fungus penetrates the bark from the bruised tissue. The cambium and phloem are discolored the least while the cortical parenchyma shows more browning. In the natural cankers, the invasion and discoloration of the bark progresses from the underlying streaks in the wood. During the awakening of the cambium, the medullary rays connecting the streak and the bark begin to discolor and the cambium directly above such cells dies and becomes distorted, while the still green bark above it is less distended than the healthy bark. The darkest discolored cambium is found above the darkest xylem rays, while at the margin of the lesion the sparsely discolored rays may show the newly formed cambium beginning to discolor. This radial form of invasion often appears in the orchard in the form of island canker or yellow streak (Plates V and VI, *B*), and can be explained as a local stimulation of a radial fungus growth from the underlying streak in the wood. It may appear about inoculations, but in these cases the cankers do not form about the abrasion but have their centers several centimeters removed from the incision. In another case (Plate XI, *B*) a continuous canker extended for 12.5 cm. with intermittent areas of green tissue and island cankers 39 cm. below and 56 cm. above the inoculation. Beneath this diseased tissue there were found prominent streaks in the outer wood that extended from the smaller twigs to the roots.

EDEMA

The formation of edematous tissue in apparently healthy bark near the margin of a canker appears to be due to a surcharging of the

underlying discolored streaks with sap, which in turn influences the bark immediately above. An examination of such turgid tissue will show that in most cases the cortical parenchyma has become many times enlarged, thin-walled, and almost devoid of chloroplasts. Sometimes at the boundary of such tissue, there may be a layer of normal parenchyma sandwiched between two layers of edematous cells.

The writer has been able to reproduce this edematous tissue under control conditions in the laboratory. (See Plate XIV.) A section of a branch was inoculated in the laboratory and after the chestnut-brown canker had formed, the end of the branch was placed in a dish of water. In a few days the characteristic edema was formed but became desiccated when the branch was removed from the water and allowed to dry. This was repeated until three distinct areas of edematous tissue had formed which, at the recession of the sap pressure, readily desiccated and collapsed.

DISAPPEARANCE OF STARCH

In the spring of the year even before the awakening of the cambium, the inoculated branches show a disappearance of the starch from the invaded tissue. Specific observations will be of interest. A pear branch in the closed cluster stage (Plate X, *B*) showed an abundance of starch in the healthy bark, medullary rays, and wood parenchyma. A few of the cells bordering the incision showed starch, while those further removed were devoid of starch. In the brown streak of the wood only isolated cells could be found containing starch when tested with iodine. In another case of a pear water sprout 7 mm. in diameter which showed a depressed canker with the line of demarcation not yet formed, there was an abundance of starch in the normal tissue. In a longitudinal section of the lesion, it was found that the outer 2.76 mm. of the discolored wood were free from starch; that next there was a region of 0.276 mm. where isolated cells were filled with starch; and finally that there was a transition zone of 0.276 mm. where the starch-containing cells were abundant, but less so than in normal healthy tissue. From the incision, the fungus advanced 0.270 mm. in the cambium and phloem, and 1.794 mm. in the inner and 1.236 mm. in the outer layers of the cortical parenchyma. The starch was absent in such invaded bark but was again present 0.590 mm. and 1.625 mm. beyond the lowest point of discoloration in the inner and outer cortical paren-

chyma, respectively. Observations made on the apple were similar to those made on the pear.

It has been shown in artificial starch cultures that starch digestion can take place several millemeters beyond the end of the mycelial threads. The dark brown to blue-green discoloration would suggest that the browning of the streaks of the apple and the blue-green discoloration of the mountain ash may be due partly to the digestive products of the fungus, and not entirely as the result of enzymatic action or oxidation of the invaded tissue. Since the apple may produce a similar brown discoloration, which is readily diffusible, it is difficult to determine the amount of discoloration directly due to the metabolic product of the fungus.

CONTROL

The environment of the host appears to be the primary consideration in canker control. Since the environment is constantly changing one would naturally expect similar changes in the results of any control measures. Such measures may be successful one year and fail in another, or even in the same year different results may be obtained in orchards remotely separated. Some of these subjects have been touched upon and hence only the more practical phases of control will here be considered.

SPRAYING

There is no known spray which will control the advance of the mycelium in the host. The deep-seated nature of the mycelium eliminates spraying as a means of canker control for no substance is known that will kill the protoplasm of the mycelium without killing the protoplasm of the surrounding bark or wood. The sprays which are usually applied by the orchardist inhibit the germination of the ascospores, but that they kill all the mycelium in the resistant stromata appears doubtful, as their presence in well sprayed orchards precludes that possibility. Since the ascospores are normally expelled from late August until the following summer, it appears impractical to advise special spraying for the control of these spores.

ORCHARD SANITATION

It is poor orchard practice to permit branches attacked with the blister canker to remain near an orchard for they may furnish a source of dissemination of the ascospores.

In 1915, branches removed from the old Station orchard were placed in a pile and were later to be used for fire wood. The upper wood dried, but that nearer the surface of the ground retained sufficient moisture to enable the fungus to form mature ascospores. It is considered a good orchard practice to remove all rubbish so as to prevent harboring insect pests and fungous diseases.

PRUNING

Pruning is a necessary annual orchard practice and the question naturally arises as to the best time for pruning. The inoculations show that the cankers form during the period extending from the opening of the blossom buds until after the petals fall. Hence, theoretically the best time to prune to control canker is after the period of blooming. However, at that time the bark readily separates from the wood and unduly large wounds may be formed, and also this period is not practical as other duties require the attention of the orchardist. General pruning should be postponed, therefore, as late as possible while the trees are still dormant. If too long an interval elapses between pruning and the radial growth, there is considerable tendency for the bark to dry back in a dry spring. Under New York conditions, it is needless to make V-shaped areas at the proximal and distil ends of pruning wounds for only in 1915 were these formed to any great degree. It is advisable that since a cut must be made with a saw, it should be properly made as close as possible to the member from which the limb is to be severed. Long stubs without saplifters dry readily and permit fungi to enter the wood and cause canker or decay.

Where it is the annual practice to cut away all dead branches, there is less tendency of cankers becoming established. Cankered branches that can be removed readily without detriment to the tree should be removed as soon as discovered. When cankers have attacked the large scaffold branches or trunk of a bearing tree, it is not so easy to advise as to the proper course. However, sooner or later the large branch will be killed by the fungus and it is merely a question of time when the branch must be removed. Some orchardists justly maintain that so long as the branch bears sufficient fruit it ought to remain, but to prevent the distribution of the disease, all branches containing stromata should be removed before the fungus becomes established in the trunk.

DECAY OF PRUNING WOUNDS

In 1915 the writer had an opportunity to obtain data on the relation of the healing of wounds and their decay. The apple trees in the Station variety orchard were dynamited in 1915 and the old pruning wounds were examined by chopping into the wounds to determine whether or not they were decayed. Table 4 gives the results of these observations. Those that showed no punky tissue were considered as sound and samples of the latter were taken into the laboratory for further examination.

TABLE 4.— NUMBER OF DECAYED AND SOUND PRUNING WOUNDS FOUND ON TREES 15 TO 45 CM. IN DIAMETER.

Description of wound	Condition	
	Decayed	Sound
Healed, all sizes	63	8
Not completely healed, over 5 cm.	53	13
Not completely healed, under 5 cm.	24	10
Painted, all sizes	5	7
Total	145	38

While a macroscopic examination of the pruning wounds showed that 21 per cent were apparently sound, when the tissues were subjected to a microscopic examination not one was found to be free from mycelium. Thus, altho externally all of these wounds appeared to be healing satisfactorily, internally they were infected by fungi. Pruning wounds that had been covered with paint two years previous showed few cracks, but beneath the paint, cracks were found in every case, indicating that the wounds were allowed to dry before applying the paint. Mycelium was always found around these cracks. Some wounds that had healed completely and that had been covered with red paint showed a high degree of cracking and decay of the heartwood. Untreated wounds 10 cm. or more in diameter always showed decay when exposed for more than two years. In longitudinal sections it can be seen that there is a conical dark brown heartwood formed from 1 to 3 cm. distant from the transverse cut and that beyond this it is converted to a mass of punky heartwood. (See Plate XV, *A*.) The degree of decay appeared to be correlated to

the amount of cracking of the wood, and it seems certain that this could be prevented somewhat by a wound dressing.

PRUNING WOUND DRESSINGS

The question is often asked whether or not it is advisable to cover pruning wounds. New York orchardists whose trees have made a luxurious growth since 1912 will regard the treatment of pruning wounds as being of very little benefit. On the other hand, orchardists of longer experience or from a different fruit district where the blister canker has been destructive, will regard wound dressings as absolutely necessary. After experiencing the accumulative effects of several years of drought (Fig. 1), the orchardist notes a preponderence of cankers about untreated pruning wounds and, thereafter, for a few years there is a greater tendency to cover the wounds.

There are certain qualifications desired in a wound dressing among which are the following: (1) The substance must be water proof in order to prevent desiccation and cracking of the wood. (2) It must be elastic so as not to crack and thus expose the bare wood. (3) It must make a close union with the wood. (4) It must not injure the bark. (5) It must be able to adhere to the slightly moist newly cut surface, for, in order to be effective, the dressing must be applied immediately after a cut is made. (6) It must be a sterilizing substance. (7) It must be cheap and practical so that it can be utilized without complicated apparatus. (8) It must be durable for the orchardist can not afford to duplicate the dressings each season.

Many substances are now recommended that have more or less value. Asphaltum has been tried and found unsatisfactory as it must be in a flowing condition when applied and this necessitates heating the substance to a high temperature. When applied to a newly made cut, it soon sloughs off; and when combined with some petroleum base as a solvent a uniform smooth surface is formed, but this also fails to adhere to the wound.

Coal tar, a product of the bituminous coal gas industry, when freed from the lighter oils does not injure the bark and is frequently employed altho there are objections to its use. However, the time of year that the tar is applied is a factor in determining its permanency for if applied in winter the smooth covering will persist until warm

weather sets in when it is absorbed. On the other hand, if applied in the summer the tar may be absorbed within 48 hours, and, the wound will then behave as an untreated wound. Tar applied to the long grain of the wood, as on the side of the trunk, may persist for from two to three years before sloughing off. In all cases its adhesiveness is dependent upon the degree of moisture present in the wood, the tar being absorbed when the tissue is dry. Grafting wax which has tallow as one of its ingredients may be pried from the cut as soon as the callus is formed. Paints free from turpentine have some of the objections of coal tar, but are less readily absorbed. Paints adhere poorly to a moist surface and for that reason it is necessary to permit the surface to dry before they are applied.

DISINFECTION OF PRUNING WOUNDS

The precaution is often taken to sterilize pruning wounds with some disinfectant before applying the wound covering. The use of creosote or carbolineum may result in injury and they should not be employed. Liquid disinfectants, such as mercury bichloride, copper sulfate, lime-sulfur, etc., are frequently applied, but these are objectionable because they moisten the surface and prevent the adhesion of paint or tar. Also, these disinfectants are only superficial and do not penetrate into the wood sufficiently to kill the mycelium. When tar is used, it has in itself the necessary antiseptic properties to sterilize the cut surface.

SHELLAC PLUS TAR AS A WOUND DRESSING

The writer has found the most successful pruning wound covering to be a coat of orange or common shellac followed in a few minutes by a coating of coal tar. The shellac, due to the fact that alcohol is the solvent, will combine with the wood of a fresh wound and thus can be used immediately after the cut is made without waiting for the surface to dry. The alcohol also acts as a surface disinfectant. Shellac in itself is considered a very good covering, but it has the objection that it may soon weather away. The application of coal tar or paint prevents this weathering. This double coating is impervious and thus prevents cracking. When compared with other dressings, it withstood the elements the best, for after four years the covering was still present. Wounds protected in this manner showed the least browning or decay of the heartwood, the least drying of the

bark, and the greatest callus formation. When taken into the laboratory and examined, a few cracks and even decay were present altho to a lesser degree than in the checks or wounds covered by other substances. The common fungus (*Schizophyllum alneum*) was isolated oftener from such tissue than was any other fungus. Macroscopically these wounds, after four years, showed the least decay, but when examined under the microscope mycelium could always be found. After careful consideration the writer concludes that it is impossible to keep a pruning wound absolutely free from fungi. The checks and those wounds covered with tar could be distinguished only by the slightly darker color of the outer surface where the tar was absorbed.

FORMATION OF WATER BLISTERS

While the shellac plus tar covering is considered superior to all other dressings, it also has its limitations. Under certain conditions, it appears that impervious coverings are a detriment rather than an asset. The writer has found that when this covering is applied to a cut made in removing a branch containing a blister canker, or to a normal branch that shows brown heartwood, the dressing will not adhere to the sap-surcharged discolored wood. In other cases it will adhere for a short time only to be loosened later by the copious sap flow from the dark wood. Eventually numerous small blisters or even one large blister may form over the discolored wood, attaining the diameter of the discoloration. These blisters are not formed over healthy sap wood. The distended watery blisters sooner or later burst and the loosened covering soon weathers away leaving the unprotected wood subject to desiccation and to the entrance of fungi.

Blisters have been formed beneath coverings of paraffin, asphaltum, coal tar, shellac, paint, shellac plus paint, and shellac plus coal tar. The exudation of sap from the blisters when prolonged is a favorable place for the growth of yeasts and molds, and the condition is known as slime flux. The opinion has been expressed, due to the odor of the sap which is similar to that accompanying fermentation, that the exudation is due entirely to fermentation organisms, however, the sap may be observed coming from fresh wounds and it is most prevalent after periods of protracted rains. That live wood is not necessary for such exudation was noted in 1914, when a copious

flow was observed from a pruning wound that, for two years had had no healthy bark nearer than 4 inches from the cut. (See Plate II.)

SURGERY

If a healthy callus has formed about a canker it should by no means be disturbed, altho the loose bark should be removed. Sometimes the removal of about 2 cm. of healthy bark from the sides of an enlarging canker may be sufficient to permit a callus to form, but at the apices less satisfactory results are obtained. Early June, when the tree is in its greatest radial growth, is the best time to undertake such experiments. Sooner or later, however, the fungus generally attacks the sides, and in one case the writer observed a callus 3 cm. thick, which was finally killed.

In Table 5 are summarized the results secured with the various methods tested for the control of the blister canker.

TABLE 5.—SUMMARY OF TREATMENTS FOR CONTROL OF BLISTER CANKER.

Treatment	Dates of treatment and final observations		Condition	
	Treated	Observed	Cankered	Healed
Surgical methods applied	1912	1914	7	1
Branches cut off below canker, covered with carbolineum and tar	1912	1914	9	4
Branches cut off below canker, untreated	1912	1914	7	0
Surgical methods applied (Baldwins)	1912–16	1912–18	5	3
Branches cut off below canker, tarred (Baldwins)	1912–16	1912–18	23	22
Branches cut off below canker, untreated (Baldwins)	1912–16	1912–18	18	8
Branches cut off below canker, shellaced and tarred (Baldwins)	1915	1918	26	11
Branches cut off below canker, untreated (Baldwins)	1915	1918	38	12

The above data have little practical bearing since each individual canker must be considered an experiment in itself as no two branches are similar in the degree of infection. Where carbolineum and tar were applied, they appeared to have injured the cambium, and externally no indication of their presence was observed at the end of the experiment. However, in hand sections it was seen that the

tar covering had penetrated the wood from 2 to 3 mm. Such transverse cuts were much cracked and functioned like untreated wounds. In some cases one-half of a canker was treated surgically, while the other half was untreated and the entire surface covered with tar. Where surgery was employed the results, temporarily, appeared to be more satisfactory, but later both halves again increased their margins at about the same rate as observed previous to the treatment. The most satisfactory results were obtained where the branch was cut off from 25 to 50 cm. below the margin of the lesion, but even then some cankers enlarged again from 2 to 150 cm. beyond the new cut. If the transverse cut is made close to the canker, the newer streaks are close to the bark and the intervening healthy wood is less than if the cut were made some distance away. The deeper imbedded streaks exert less influence in inhibiting the radial growth of the cambium directly above such streaks and thus present a better opportunity to occlude the fungus. Where the streaks are close to the bark, a feeble callus is formed which is later killed by the fungus. (See Plate VII, *A*.) The inoculations also showed that if the mycelium is in the vicinity of the bark, cankers will result even tho the wounds are well covered with a dressing. Hence, the success of a canker treatment depends upon the amount of healthy tissue remaining between the diseased streaks and the healthy bark thus permitting the fungus to be readily occluded, rather than upon any dressing which may be applied either to the canker or the wound.

PRESERVATION OF SOIL MOISTURE

Any orchard practice which stimulates callus formation may be considered as aiding the host to occlude the fungus. If streaks are well imbedded in the wood, it is essential for canker control that the soil moisture be conserved in order to produce maximum radial growth. Should a drought condition exist at the time the buds are swelling and extend into June, as was the case in 1915, there will be an increase of fungus activity. The influences of such a period are not limited to one season, but when combined with the inhibition of radial growth produced by the presence of the fungus, the effects are noticeable from two to three years after and cankers will enlarge in spite of the best surgical methods that may be employed. Abnormal rainfall at this critical period results in more abundant radial growth with a greater tendency for the fungus to be occluded.

altho if the mycelium is close to the bark, cankers will form in spite of the heavy rains. Therefore, early cultivation, if practicable, is advised, especially in a period of limited rainfall. If the orchard responds to fertilizers, late fall plowing of a cover crop or an application of barnyard manure in March or April will stimulate growth providing there is sufficient moisture to render available the chemical food constituents.

CONCLUSIONS

The data here presented establish the pathogenicity of the fungus *N. discreta* as the causal agent of blister canker of apple. Observations dependent upon natural cankers lead to unwarranted conclusions unless supplemented by observations of cankers artificially induced. In the case of the natural cankers, the extension of the lesions did not appear to follow any definite course which would hold under duplicated conditions. At certain times, the lesions would enlarge in a period of apparent drought, while other lesions on the same tree may show a similar enlargement during a period of protracted rainfall. Naturally, this led to confusion which was only clarified by a study of artificial cankers produced by inoculation. These cankers made their first external appearance at the time of the awakening of the cambium which coincides with the closed cluster stage of the terminal flower cluster. The uniformity of the results of the inoculations established the fact that at the time of new growth in the spring the apple tree was particularly susceptible to infection. It had already been noted that the natural cankers did not have a tendency to enlarge at this time but increased their margins later in the season. This difference is explained when one considers the proximity of the mycelium to the bark in the two cases. When inoculation is made in the dormant period of the tree's growth the mycelium comes in direct contact with the cambium tissue. In the case of the natural cankers there is generally more or less of the wood formed in radial growth intervening between the mycelium and the bark. The greater the distance between these two the longer will the time of canker enlargement be postponed. Hence, in a season of rapid growth the mycelium may be deeply occluded and the lesion heal completely, whereas, in a season of restricted growth, the callus is not of sufficient thickness to prevent the mycelial invasion. In a dry season radial growth may be checked early, while in other

cases it may be prolonged until August. Therefore, the general observation has been made that a lack of water stimulates canker formation, while an ample water supply prevents the enlargement of the lesions. It is evident, however, that in this erroneous conclusion the contributary rather than the direct cause is observed. It was shown that the actual water content of the tissue involved plays no part in canker formation when artificially induced cankers formed at a time when there was a superabundance of rain in the early spring. The subject of the water content of the tissues will be discussed further in a paper where more detailed information can be presented.

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Plate I

Red Astrachan apple tree, photographed May 31, 1912, badly attacked by the fungus *N. discreta* and showing the characteristic staghead.

PLATE I.

Plate II

Same as Plate I, photographed October 26, 1914. The dead branches were removed in 1912. The branch to the right shows a newly formed staghead due to the presence of the blister canker. Some of the lateral branches dropped their foliage before the margin of the canker reached them. Near the base of the branch is shown the effect of the yellow streak and in 1912 the stromata were abundant in the loose bark. The canker extended down the trunk and killed the roots directly below.

PLATE II.

Plate III

Photograph taken September 1, 1916, of the trunk of a Baldwin apple tree infected prior to 1900 with the blister canker fungus. The strings indicate the various margins of the advancing fungus. (See page 19.)

Plate III.

Plate IV

Photograph taken August 31, 1916 of a Collamer apple tree infected prior to 1909 by the fungus *N. discreta*. The strings outline the margins of the advancing fungus. (See page 18.)

Plate IV.

Plate V

Same as Plate IV, photographed May 9, 1917, showing the yellow streak that had formed in the previous autumn.

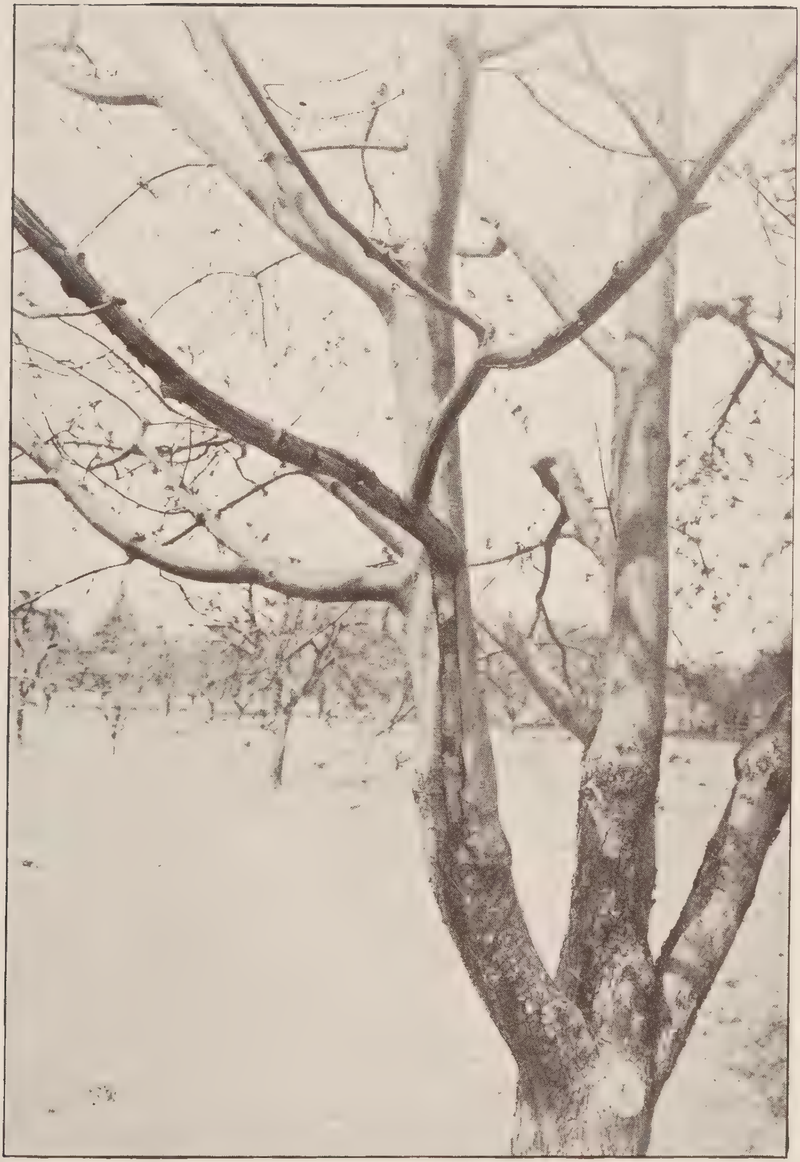


Plate V.

Plate VI

A Photograph taken June 23, 1914 of a Pomona apple tree 9 cm. in diameter half girdled by the fungus *N. discreta*. Stromata were abundant about the pruning wound made in 1911. The illustration shows the progress of the fungus and the loose cracked nature of the bark.

B The margin of the canker shown in *A*, showing the formation of the island cankers formed 115 cm. from the pruning wound. The transverse cut of a lateral branch shows the position of the diseased streaks in the wood. In the leader, the streaks extended 152 cm., being longest in the 1911 wood. Reduced one-third.

A

B

Plate VI.

Plate VII

A Newly formed blister canker showing stromata and weak callus that was killed as the fungus advanced. Natural size.

B and *C* apple trees inoculated with *N. discreta* showing the tendency of the streaks to form on lateral sides of the incision. Natural size.

D Shows the degree of discoloration formed about the check. Natural size.

A *B* *C* *D*

PLATE VII.

Plate VIII

A Photograph taken June 16, 1919, of a 7-year old Ben Davis apple tree inoculated April 28, 1917, which formed a canker resembling the condition known as sunscald.

B Same as *A*. Reduced one-third.

A *B*

PLATE VIII.

Plate IX

Transverse sections of tree illustrated in Plate VIII.

A At point of inoculation.
B At distal end of canker.
C At proximal end of canker
D At 9 cm. below *C*.

In *C* it is noted that the radial growth has been inhibited where the streaks were most abundant, and in *D* no dark duramen or discoloration of the center of the tree is produced.

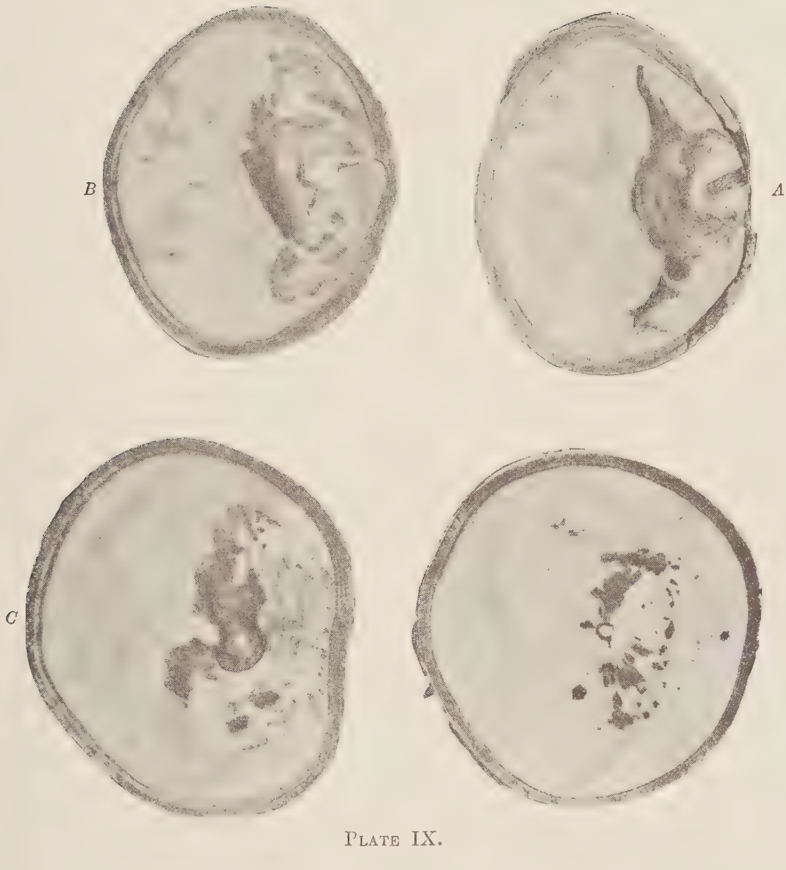


PLATE IX.

Plate X

A Longitudinal and oblique section of apple branch showing the streaks formed by the fungus *N. discreta*. Natural size.

B Photograph taken May 4, 1917, of pear showing the relation of the canker formation to the size and stage of the flower blossom. The inoculation was made April 4, while the leaf buds were 1 cm. long and showed green tissue between the scale leaves. Edematous tissue was beginning to form at the distal end of the canker.

A

B

PLATE X.

PLATE XI

A Photograph taken April 24, 1917, of an apple branch cankered by the fungus *N. discreta*. It was inoculated (at *a*) October 18, 1915, and produced a canker 24.8 cm. long in the spring of 1916. The line of demarcation had not been completed at the ends.

B Photograph taken June 20, 1916, of a 3-year old Ben Davis tree inoculated (at *a*) on April 20, with *N. discreta*. The tree was grown in the greenhouse and received an amply supply of water. A canker was formed 12.5 cm. long with island cankers 39 cm. below and 56 cm. above the inoculation.

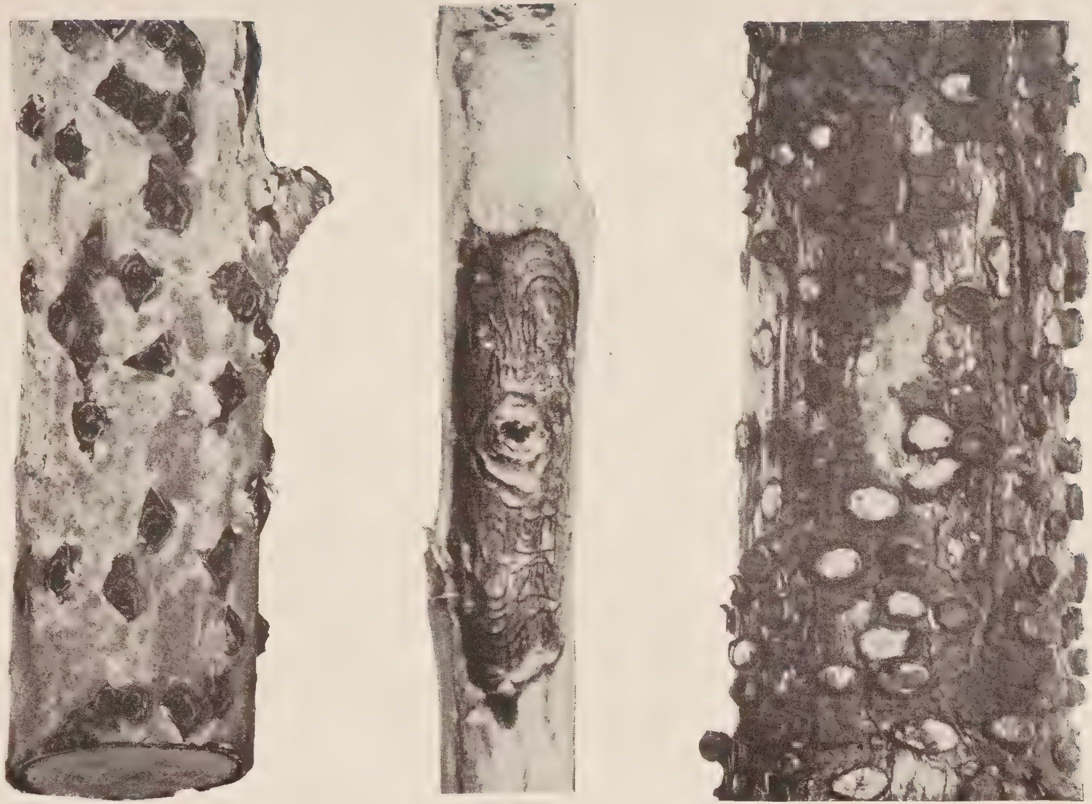
PLATE XI.

PLATE XII

A Photograph taken October 6, 1915, of mountain ash (*Sorbus aucuparia*) attacked by *N. discreta.* The stromata were covered with heaps of ascospores. Natural size.

B Blister canker formed on Ben Davis tree inoculated with a strain isolated from the mountain ash. The darker irregular concentric lines indicate the various advances the fungus made during intermittent warm and cool days. Enlarged one-half.

C Stromata of *N. discreta* on mountain ash from which the bark has weathered away exposing the bare wood. Natural size.



A *B* *C*

PLATE XII.

Plate XIII

A Photograph taken September, 1912, of apple branch showing the ascospores upon the surface of the stromata. A few stromata have been removed to show the lighter areas outlined by the darker sclerotic tissue that forms the boundary of the stromata. Natural size.

B The stellar openings of the stromata of *N. discreta* formed by the curling back of the periderm of the apple bark to expose the conidiophore cushion on the underside of the periderm and on the upper surface of the stromata. Natural size.

C An apple branch showing the margin of a yellow streak in the bark and the relation to the dark brown diseased streaks in the wood beneath the apparently healthy bark. Natural size.

B C

PLATE XIII.

Plate XIV

A portion of an apple branch inoculated in the laboratory with *N. discreta*.

After a small canker (*a*) had formed, the branch was set in a dish of water and the edematous yellow streak (*b*) developed. The branch was then allowed to dry partly and another zone (*c*) was formed and when again placed in water the last or outer zone (*d*) was produced.

Plate XIV.

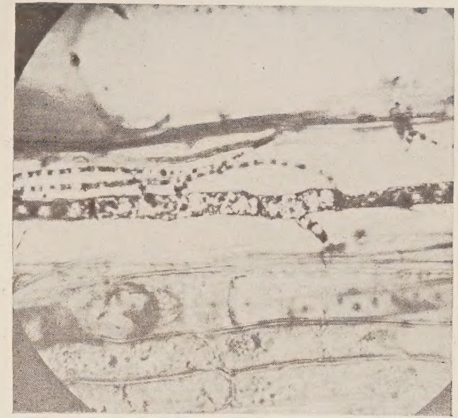
Plate XV

A Longitudinal section of a pruning wound that showed badly decayed heartwood in spite of the fact that the wound had completely healed over. Natural size.

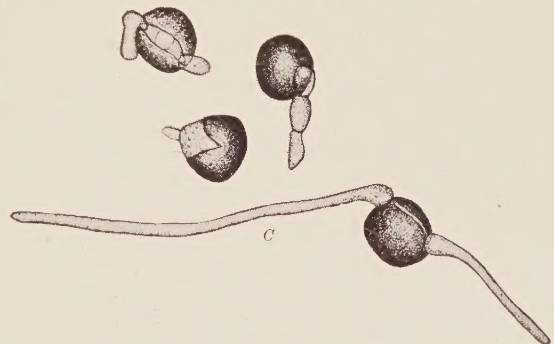
B Longitudinal section of brown discolored streak of the wood showing the mycelium in the tracheal tube.

C Various forms of ascospore germination.

A



B



C

PLATE XV.